SYSTEMATICS OF THE MARMORATUS GROUP OF THE FROG GENUS *LEPTODACTYLUS* (AMPHIBIA, LEPTODACTYLIDAE)[1]

By W. Ronald Heyer[2]

Abstract: The geographic distribution patterns of eight characters of size, shape, texture, and color pattern were examined for members of the Marmoratus species group of the frog genus *Leptodactylus*. Analysis of the geographic distribution of character states indicates that the group is composed of five species. *Leptodactylus bokermanni,* new species, has nonexpanded toe tips and occurs in the forests of southeast Brasil. *Leptodactylus hylaedactylus* has nonexpanded or slightly expanded toe tips and inhabits the forests of greater Amazonia and southwestern Brasil. *Leptodactylus andreae* has toe disks and occurs in the Orinocan and greater Amazonian forests. *Leptodactylus marmoratus* has toe disks and occurs in the forests of southeastern Brasil. *Leptodactylus martinezi* has nonexpanded toe tips and inhabits the dry forests of central Brasil. Each species is diagnosed and described, and a key is provided.

It is hypothesized that the foam nest in the Marmoratus group and that of the other species groups in the genus *Leptodactylus* evolved in response to different selective forces. In the case of the other species groups, the foam nest has evolved in reponse to arid conditions with sporadic heavy rain. In these situations, rainfall can be used in a predictive manner to ensure reproductive success. In the Marmoratus group, rainfall may not be a good predictor of reproductive success. Terrestrial organisms have a relatively stable reproductive environment in wet tropical forests, however. The foam nest in the Marmoratus group apparently has developed as a response to selection for terrestriality.

Introduction

This paper is the second of a projected series on the systematics of the species groups of the genus *Leptodactylus*. The first treated the Melanonotus group (Heyer, 1970a); the present paper treats members of the Marmoratus group as previously defined by Heyer (1968). The members of this group have been poorly understood, both with respect to how many species comprise the group and to what the relationships of the Marmoratus group are to the other species groups within the genus. This paper is addressed to the first problem.

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The reviewers of this paper do not all concur that the methods of analysis used are the most appropriate. That decision, as well as all interpretations, remains solely mine.

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Methods and Materials

Over 1300 preserved specimens form the basis of this analysis. Early in the study, it became clear that the problem could best be treated in the manner used by Gans (1959, 1966). The analysis was done in three stages; in the first, the following were recorded:

1) Sex. Individuals were determined to be either male, female, or juvenile. Males were determined by the presence of vocal slits. Females were determined by presence of eggs visible through the ventral body wall, or by size if males were present from the same locality. If there was any question, the individual was scored as a juvenile.

2) Size. The snout-vent length was measured to the nearest 0.1 mm with vernier calipers.

3) Snout shape. A ratio was determined which in selected samples reflects the differences between blunt and pointed snout shapes. A specimen was lined up under a grid-type ocular micrometer in a dissecting microscope so that one line traversed the distance between the anterior corners of the eyes. This distance was read and used as the denominator. The numerator was determined by reading the distance at right angles from the grid line connecting the anterior eye corners to the tip of the snout. The larger the value of the ratio, the longer the snout.

4) Toe tip shape. Four categories of toe tip shape were recognized, ranging from

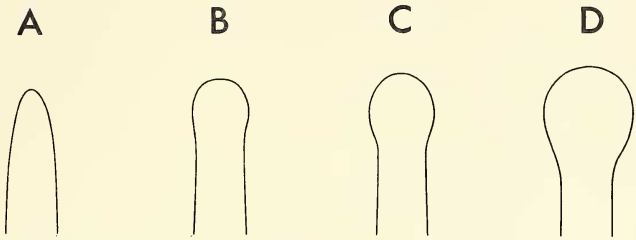

FIGURE 1. Toe tip character states, see text.

state A, the tips pointed, to state D, the tips with large, distinct disks (Fig. 1). In this character only, intermediate categories were used, such as B–C or C–D.

5) Dorsal texture. Four character states were recognized: A, dorsum smooth; B, Dorsum with white tipped tubercles; C, dorsum with ridges or warts; D, dorsum with dorsolateral folds and white tipped tubercles. The method of preservation affects this character. Many of the specimens scored as having state A certainly had one of the other states in life. Because of this, the variation of dorsal texture was not analyzed in detail, but the range of variation is described in the individual species accounts in a later section.

6) Dorsal pattern. Six different character states were recognized (Fig. 2). Here,

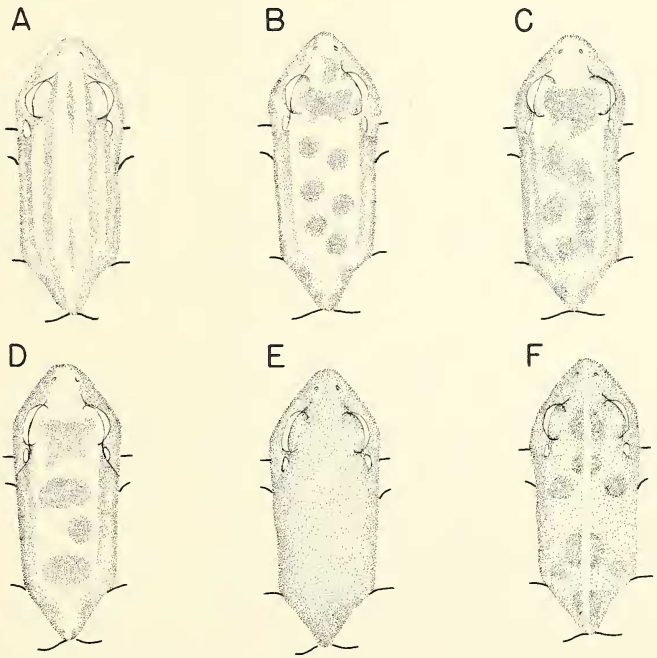

FIGURE 2. Dorsal pattern character states, see text.

as in the other characters which were broken down into arbitrary states (with the exception of toe disks), a specimen with an intermediate category was placed into the category it most resembled.

7) Dorsolateral stripes. Three states were recognized: A, no dorsolateral stripes; B, light, narrow, dorsolateral stripes from the eye to the inguinal region; C, light, broad, conspicuous dorsolateral stripes from the eye to the inguinal region.

8) Light mid-dorsal stripe. Seven states were recognized: A, no mid-dorsal stripe; B, a mid-dorsal pin stripe from above the vent to about midbody; C, a pin stripe from above the vent to the snout; D, a stripe wider above the vent, tapering to a point not beyond the sacrum; E, a broad stripe from above the vent to the tip of the snout; F, a pin stripe from above the vent not extending beyond the sacrum; G, a wide stripe in the sacral region only.

The specimens were examined locality by locality. As the first stage of analysis was being done, the specimens from each locality were examined to determine if there were one or more distinctive forms; that is, specimens exhibiting consistent discontinuous variation in two or more characters. Localities of presumed instances of sympatry of two distinctive types were noted. Detailed comparison of the specimens from the presumed sites of sympatry formed part of the second stage of analysis. This part of the analysis, termed "the recognition of non-dimensional species" by Gans (1966), centers about study of sympatric occurrences. Distinctive specimens from the same locality are examined in detail. Samples from surrounding localities are then compared with and determined to be one or the other distinctive forms from the site of sympatry. This was done separately for each of seven large areas.

The third stage of analysis, termed, "the recognition of species in space" by Gans (1966), involves detailed analyses of similar forms over the entire geographic range. Decisions are made as to how many species are represented based on this third stage of analysis.

This methodology is nothing more than standardized common sense as historically used in systematics. It is not a phenetic analysis in the numerical taxonomy sense, but rather a "classical" taxonomic approach. The reason for utilizing the methods outlined by Gans (1959, 1966) is that it allows one to keep track of variability when large numbers of specimens over wide geographic areas are being studied.

The Recognition of "Non-Dimensional" Species

Seven large areas were delineated to form the study units for the recognition of "non-dimensional" species. Each area was determined on the basis of at least one locality where two forms occurred together, proximity of other localities from which specimens originated, amount of material, and intuition. The situation for each area follows.

Area A—This area consists of lands of north draining rivers. A single instance of sympatry was found (Surinam; Nickerie, Sipaliwini, Fig. 3, number 1). The forms are distinctive when closely compared (Fig. 4). The forms are designated as I and II and differ as follows. Form I (11 specimens) is more robust than form II (4 specimens); form I has either a uniform dorsum or wide saddlelike dark blotches, form II has more or less distinct small spots dorsally; 1 specimen of form I has type C dorsolateral

FIGURE 3. The seven study areas for recognition of "non-dimensional" species. Numbers indicate localities where more than one form is represented in collections.

stripes, none of the form II specimens has dorsolateral stripes; the snout of form I males is sharply pointed in profile, the snout of form II males is rounded in profile; the toe tips of form I specimens are either type C or D, the toe tips of form II specimens are type B, or type B almost type C; the dorsum is smooth in all form I specimens, the dorsum in a single form II specimen is warty. Specimens from all localities within Area A were readily allocated as either form I or II using the Sipaliwini specimens as standards.

Area B—This area covers the Brasilian territory and states of Amapá, Mato Grosso, Pará, and Goiás which are drained by the Amazon or Tocantins river systems. Instances of sympatry are at Amapá; Serra do Navio 220–300 m, Serra do Veado, 290–310 m (Fig. 3, number 2), Mazagão (Fig. 3, number 3); Pará; Belém (Fig. 3, number 4), IPEAN, 3 km E Belém (Fig. 3, number 5), and Cachimbo (Fig. 3,

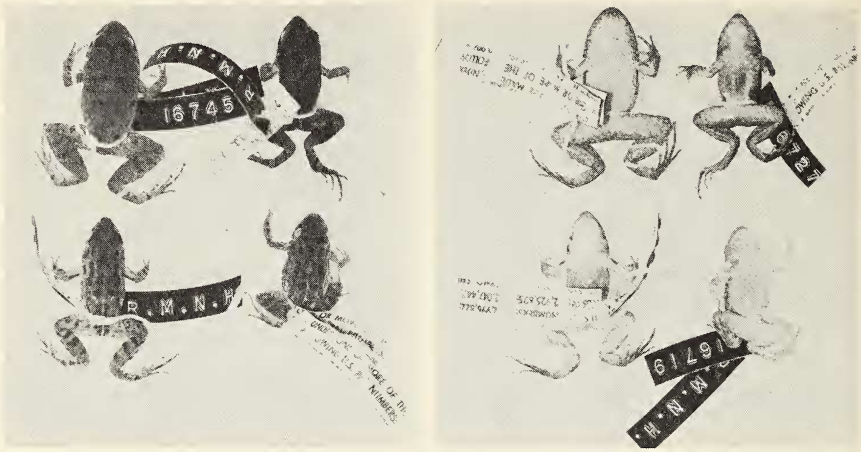

FIGURE 4. Frogs from locality one of Fig. 3. Left—dorsal views; upper two specimens are form I individuals, lower two form II. Right—ventral views; upper two specimens are form I individuals, lower two form II.

number 6). At each site except Cachimbo, there are two forms, which are again designated as I and II. Here and in the other major areas, designation of I forms indicates that the I form of Area A is most similar to the I form of Area B, but relationships among all the I forms from all areas constitutes the analysis of the species in space of the next section. The sympatric I forms of Area B (143 specimens) differ from the II forms of Area B (17 specimens) as follows: the body shape of form I specimens is slightly more robust than in form II specimens, but the differences are not as pronounced as in Area A; the dorsal patterns of form I specimens are more uniform, the dorsal patterns of form II specimens are more mottled with a tendency toward spotting; the venters of form I specimens are darker than in form II specimens; some form I individuals have broad, light dorsolateral stripes, no form II individuals have such stripes; no form I specimens have B or C category light mid-dorsal stripes, while some form II individuals do; the toe tips of form I individuals are C or D category (Fig. 1), the toe tips of form II individuals are either B or C category (Fig. 1)—in the C cases of both forms the disks are distinctive in that the C category disk of form I is flattened while the C category disk of form II is rounded (Fig. 5). At Cachimbo, two distinctive forms were recognized. The first corresponds to the II form of Area B. The second corresponds to the F dorsal pattern of Figure 2 and is designated form III. This is the only site where more than one distinctive form is known to occur in which both forms have no disk development of the toes. The specimens from all other localities from within Area B. were readily designated as being either form I, II or III. The form I specimens from Pará, Jacareacanga have notably large toe disks.

Area C—This area includes samples from the Brasilian state of Amazonas. Instances of sympatry were found at Itapiranga (Fig. 3, number 7) and Ducke Reserve, near Manaus (Fig. 3, number 8). At both sites, the different forms consisted of forms I and II. The differences between form I (7 specimens) and form II

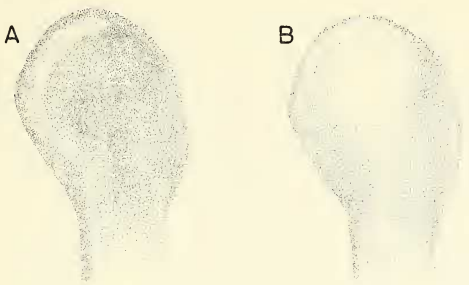

FIGURE 5. A, C category of toe disk of form I individuals. B, C category of toe disk of form II individuals.

(5 specimens) at the two sites of sympatry are: some form I individuals have light, broad dorsolateral stripes, no form II individuals have such stripes; no form I specimens have B or E category mid-dorsal light stripes, some form II specimens do; form I individuals have C or D category toe tips, form II individuals have B category toe tips. Individuals from all other localities within Area C were readily distinguished as either I or II forms using the specimens from localities 7 and 8 (Fig. 3) as standards with the exception of the specimens available from Manaus. These 4 particular individuals are so desiccated that proper allocation is not possible.

Area D—This area includes samples from the Brasilian state and territory of Acre and Rondônia. Two sites of sympatry were identified: Rondônia, Pôrto Velho (Fig. 3, number 9) and Igarapé Marmelo (Fig. 3, number 10). At Pôrto Velho, two forms were present, I (4 specimens) and II (9 specimens) which differ as follows: two form I individuals have broad, light, dorsolateral stripes, no form II individuals have such stripes; no form I individual has an E category light mid-dorsal stripe, one form II individual does; form I individuals have C or D category toe tips with flattened disks (Fig. 5A), form II individuals have category B or C toe tips, if category C, the disks are rounded (Fig. 5B). Specimens from other localities within Area D were readily identified as either form I or form II using the Pôrto Velho specimens as standards with the exception of the specimens from Igarapé Marmelo. Igarapé Marmelo is the only locality where intermediate individuals between form I and form II types were identified for any of the areas. Three individuals are clearly the same as form I individuals from the other localities within Area D with respect to toe disk development. Seven individuals are clearly the same as form II individuals from other Area D localities in toe tip development and in some individuals having B, C, and E categories of mid-dorsal stripe development (Fig. 6). Two individuals are intermediate with respect to toe tip development. In addition, the dorsal patterns are complex and not easily described in the total sample, but the form I specimens tend towards uniformity, the form II specimens tend toward spotting, while the two individuals intermediate in toe disk development appear to be a combination of both form I and II patterns (Fig. 6).

Area E—This area includes Amazonian localities from Colombia, Ecuador, and Peru. Two instances of sympatry were noted: Peru; Loreto, Iparia (Fig. 3, number 11) and Peru; Pasco, Iscozazin Valley, Pan de Azucar (Fig. 3, number 12). Seven form I

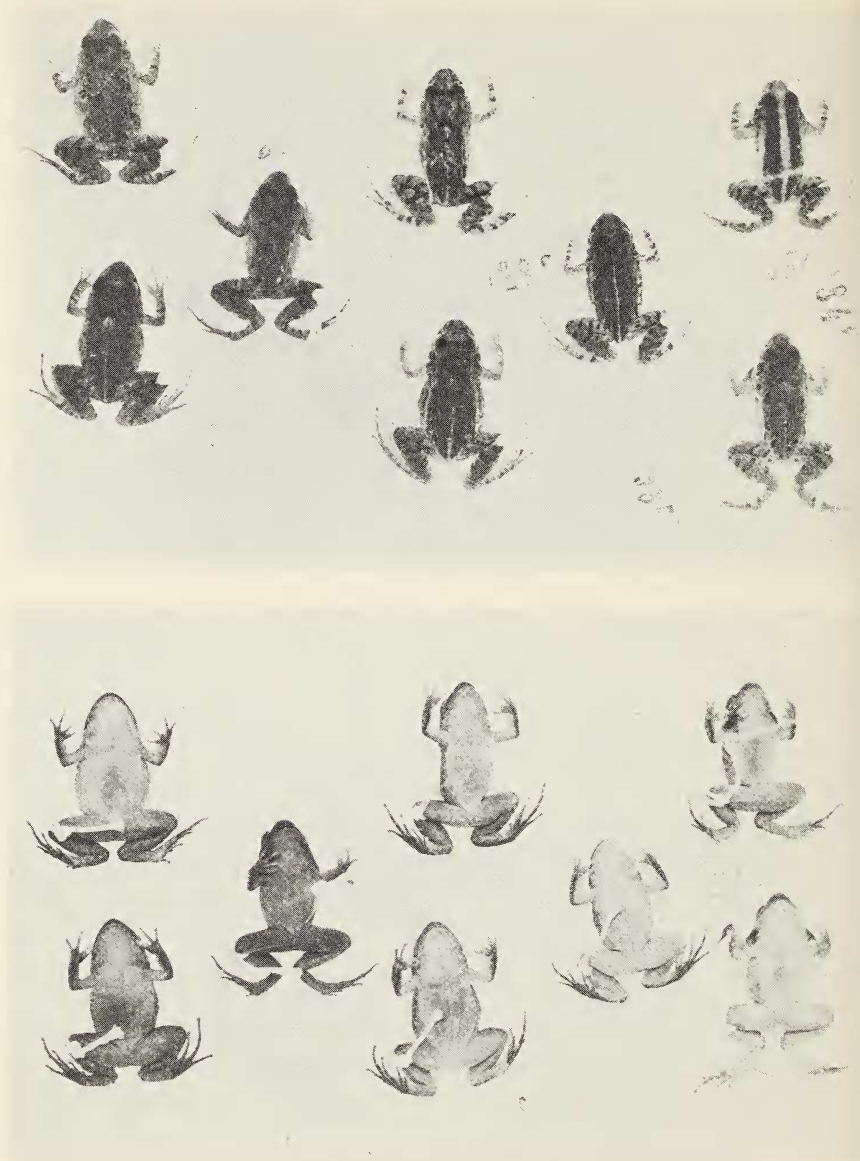

FIGURE 6. Specimens from Igarapé Marmelo, Territorio do Rôndonia, Brasil. Specimens on left of upper (dorsal view) and lower (ventral view) figures are form I individuals; specimens on right are form II individuals, specimens in middle are intermediates.

individuals differ from nine form II individuals at the two localities in the following: form I individuals have broader heads than form II individuals; the dorsal surfaces of form I individuals are uniform except for a posterior continuation of the dark interorbital blotch, the dorsal surfaces of form II individuals are fuzzy-spotted; no form I individuals have category B light mid-dorsal stripes, some form II individuals have the B category stripe; the ventral surfaces of the thigh and calf are darker in form I individuals, lighter in form II individuals (Fig. 7), the toe tips of form I individuals are category C, form II individuals are category B. Individuals from all other localities in Area E were readily categorized as either I or II forms using the specimens from the two sites of sympatry as standards. In this area, dorsal and particularly ventral pattern proved more useful than toe tip shape in separating the two forms.

Area F—This area includes all samples from Bolivia. One instance of sympatry was noted, Bolivia; Santa Cruz, Buenavista (Fig. 3, number 13). Differences between the form I specimens (31) and form II specimens (39) are: dorsal surfaces of the form I specimens are more or less uniform in pattern, the dorsal surfaces of the form II individuals are blotched, not quite forming distinct spots; some form I individuals have broad, light dorsolateral stripes, no form II individuals have such stripes; no form I individuals have B or C category light mid-dorsal stripes, some form II individuals do; the snouts of form I males are pointed in profile, in form II males the snout profiles are rounded; form I specimens have C or D category toe tips, most form II specimens have category B toe tips, a few specimens have toe tips approaching the C category; two form I individuals have dorsolateral folds, no form II individuals have dorsolateral folds. All other samples from Area F were readily categorized as either form I or II using the Buenavista individuals as standards with the exception of a single individual from Santa Cruz, Río Ichilo, 34 km S Boca Chapare. In this instance, determination was made on the basis of dorsal pattern as the toe tips were not clearly either B or C category.

Area G—Area G covers all lands drained by rivers that empty to the east or south of Brasil and southern South America. A single instance of sympatry was found:

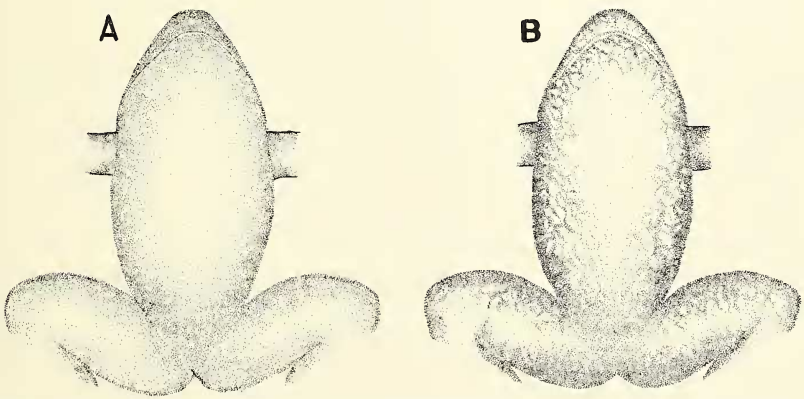

FIGURE 7. Ventral patterns of frogs from area E. A, form II individual, B, form I individual.

Brasil; Rio de Janeiro, Teresópolis (Fig. 3, number 14). The specimens from this locality are poorly preserved, making detailed comparisons impossible. One specimen from this series clearly has the C type category toe tips while the other nine specimens clearly have the B type category; the single form I individual also has broad, light dorsolateral stripes, none of the form II individuals have such stripes. Specimens from most other localities were categorized as either I or II forms, but specimens from several localities were difficult to allocate. First of all it was evident that more than one type of II form was involved. The form II individuals from the coastal states of Guanabara, Minas Gerais, Rio de Janeiro, and São Paulo differ from form II individuals from Goías and Mato Grosso. The latter specimens are more similar to the form II individuals from Amazonas and Pará. None of the coastal form II individuals have a dorsal pattern of distinct spots nor do any individuals have B, C, or E category light mid-dorsal stripes. Further, some individual specimens in series from Guanabara; Rio de Janeiro, Tijuca, and Cosme have very poorly developed disks but seem to be form I specimens. The most difficult situation to interpret at this point is some of the specimens from Parana. The form I individuals from the southern part of the state of São Paulo and the state of Santa Catarina are quite small and have well-developed disks. Most of the Parana specimens are larger with no disk development at all. These same specimens have broad, light dorsolateral stripes, which throughout all the other study areas were found only in form I individuals. Because of the broad, light dorsolateral stripes, the specimens from Parana are included in with the form I specimens for further analysis in the next section.

DISCUSSION

At this point it is appropriate to ask whether at each site of sympatry, the different forms represent a single species polymorphic system, or the different forms represent distinct species. To help reach this decision, presentation of the only mating call recordings is necessary. Werner Bokermann kindly sent me audiospectograms of four individuals of the Marmoratus group from recordings he took in the field (Figs. 26, 28). One audiospectogram is from a form I individual (Fig. 28), the other three were recorded from form II individuals. All recordings are based on allopatric specimens. I interpret the audiospectograms as representative of two call types, correlating with the different morphological forms. Detailed descriptions of the calls will be presented elsewhere.

Levins (1968) discussed a theoretical situation involving polymorphism within a single species which could account for the situation presented here. In Levins' terms, a species with a concave fitness set living in a coarse grained environment will be polymorphic, and the morphs might be mistaken by systematists for closely related species. Briefly, this would mean that two distinctive environments occur in such a pattern that an individual is likely to spend its entire lifetime in a patch of a single kind. The alternative environments are very different compared to individual tolerance, so the population strategy is to have two morphs, each adapted to one environmental type. In practice, Levins states that such organisms demonstrating this strategy would most likely be small organisms with reduced mobility. If frogs demonstrate the pattern

proposed by Levins, then members of the Marmoratus group are likely candidates. The system described by Levins implies that the polymorphism is controlled by very few genes. At most of the sites of sympatry, two forms were recognized, I and II, which differed in dorsal ground pattern, development of dorsolateral stripes, development of mid-dorsal stripes, development of toe disks, and apparently mating calls. One would have to assume either that several groups of genes or a few pleiotropic genes are involved. It is probably most reasonable to assume that several different groups of genes are controlling the differences between form I and II individuals. This in turn suggests that form I is a species distinct from form II in each of the major study areas. Form III is very distinct from either I or II so that it probably is representative of a distinct breeding unit. The one exception to the discussion involves the specimens from Brasil: Rondônia; Igarapé Marmelo. This was the only locality where intermediates between form I and form II individuals were recognized. Due to the distinctiveness of the forms at all of the other localities, I interpret the situation at Igarapé Marmelo to represent hybridization between two closely related species. The results of this portion of the analysis are the recognition of three "non-dimensional" species correlating to forms I, II, and III as recognized above. The next analytic procedure will attempt to determine whether all species I populations from each major study area represent the same species and whether all species II populations from each major study area represent the same species.

THE RECOGNITION OF SPECIES IN SPACE

Small samples are available for species III which are rather uniform. No further analysis of variation is presented for this species. The character states for the I and II forms were plotted separately. Plotting was done on map overlays so any geographic trends could be noticed. Samples within a 150 km circle diameter area were combined in cases where no differences were noted among the samples during prior examination. For numerical data, when individual samples consisted of 10 or more individuals, the standard error was determined for that sample. For male and female sizes, the sample mean and maximum were plotted for each locality. Such trends are not necessarily statistically significant, but may indicate differences. The reasoning here is that any populational variation may be helpful in determining the status of the populations. The determination of the status of the populations depends on a value judgment of all known trends and variables. That is, the results of this analysis do not in themselves provide any answers, but they do provide data from which more intelligent inferences may be drawn.

Analysis of Form II Specimens

Male size—Form II males range in size from 19.4–26.2 mm S–VL (snout-vent length). There were only three samples which had 10 or more males: These are from French Guiana, Bolivia, and the state of São Paulo, Brasil. The samples from French Guiana and Brasil differ by one standard error. The overall trend demonstrates a slight difference in size between the Peruvian and Bolivian samples, the Peruvian samples having the largest individuals examined (Fig. 8). The smallest males examined come

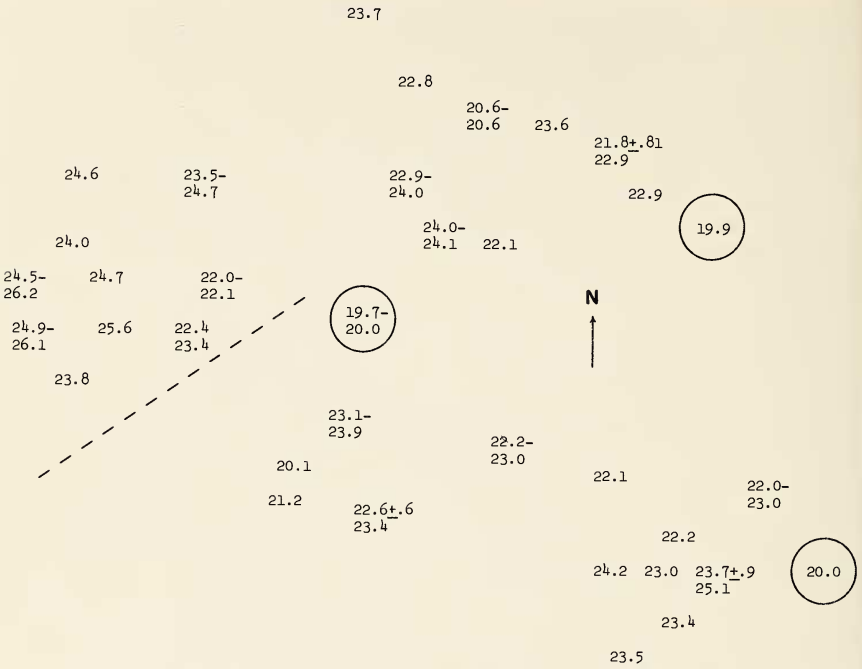

FIGURE 8. Relative geographic distribution of male size of form II individuals. Single value indicates length of single individual; one value immediately below another indicates the upper value is the mean based on 2 to 9 individuals, the lower value is the maximum; the addition of one standard error indicates a sample size of 10 or more. See text for further explanation.

from three different Brasilian localities: Pará, near Belém, Rondônia, Pôrto Velho, and Rio de Janeiro, Teresópolis (Fig. 8).

Female size—Form II females range in size from approximately 20 mm to 31.0 mm S–VL. Four localities were analyzed with 10 or more individuals: French Guiana, 22.5 (mean) ± 1.5 (one standard error) mm, Peru; Departamento de Huanuco, 23.9 ± 2.0 mm, Bolivia; Departamento de Beni, 22.7 ± 1.8 mm and Bolivia; Estado do Santa Cruz, 23.2 ± 1.8 mm. The only noticeable trend is that the largest individuals come from the states of Huanuco and Pasco in Peru and from Peru: Loreto; Suhuaya, near Contamana on Río Ucayali.

Male snout ratio—Three locality samples of 10 or more individuals were available: French Guiana, Bolivia, and from the state of São Paulo, Brasil (Fig. 9). There are no statistical differences among these samples. The only noticeable geographic pattern is that males with high snout ratios are found in central Mato Grosso and southern Goiás, Brasil (Fig. 9).

Female snout ratio—The female snout ratio is consistently smaller than the male snout ratio at any individual locality. The four localities adequate for statistical considerations are: French Guiana, Cayenne and surrounding area, .68 (mean) ± .04 (one standard error), Bolivia, Beni, Huachi and surrounding area, .67 ± .06, Bolivia; Santa

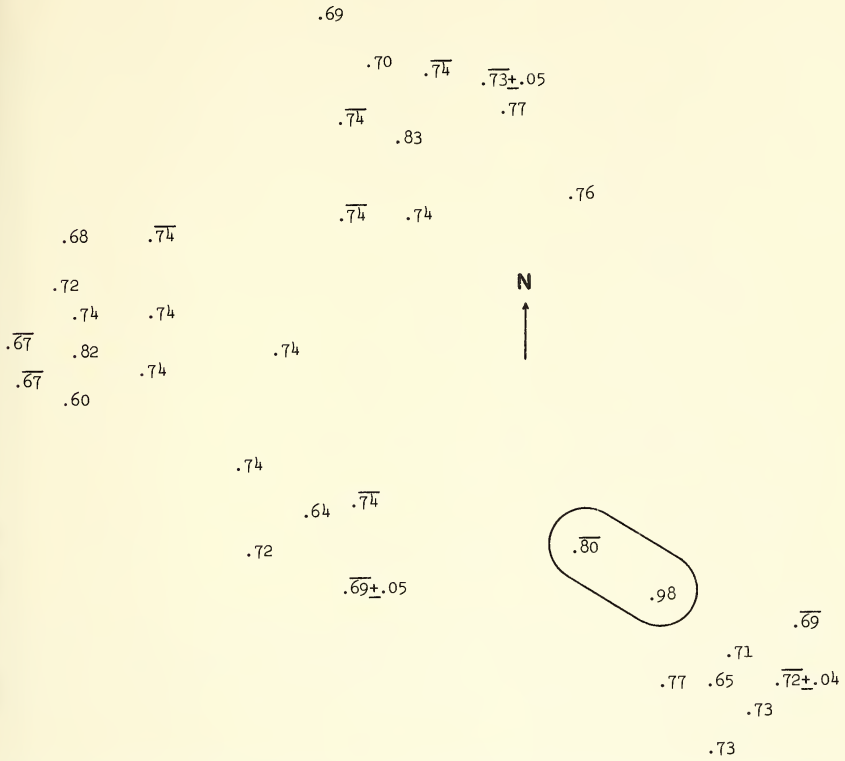

FIGURE 9. Relative geographic distribution of male snout ratios of form II individuals. Individual values are where a single specimen is represented; a horizontal bar above the index value indicates a mean value of 2 to 9 individuals represented; a horizontal bar and a plus or minus value is the mean value and one standard error for 10 or more individuals from a given locality. See text for further explanation.

Cruz, Buenavista, .67 ± .04, and Peru; department of Huanuco samples, .64 ± .06. No geographic patterns are evident.

Dorsal pattern—There are no absolute differences in patterns, but certain trends are clear. Almost all of the populations north of Amazonia have a large percentage of B category pattern, as do certain Brasilian populations in the territory of Acre and the states of Mato Grosso and Goiás (Fig. 10). Remaining populations are characterized by a preponderance of E category patterns. A single individual from near Belém was categorized as D.

Dorsolateral stripes—Populations from the Brasilian territory of Amapá, French Guiana, Surinam, southern Guyana, and the localities of around Feijó, Acre, Brasil; Río Perene, Junín, Peru; and Belo Horizonte, Minas Gerais, Brasil have a high incidence of B category individuals (Fig. 11). Two northernmost populations have C category individuals. In these instances, the stripes begin at the shoulder, not the eye

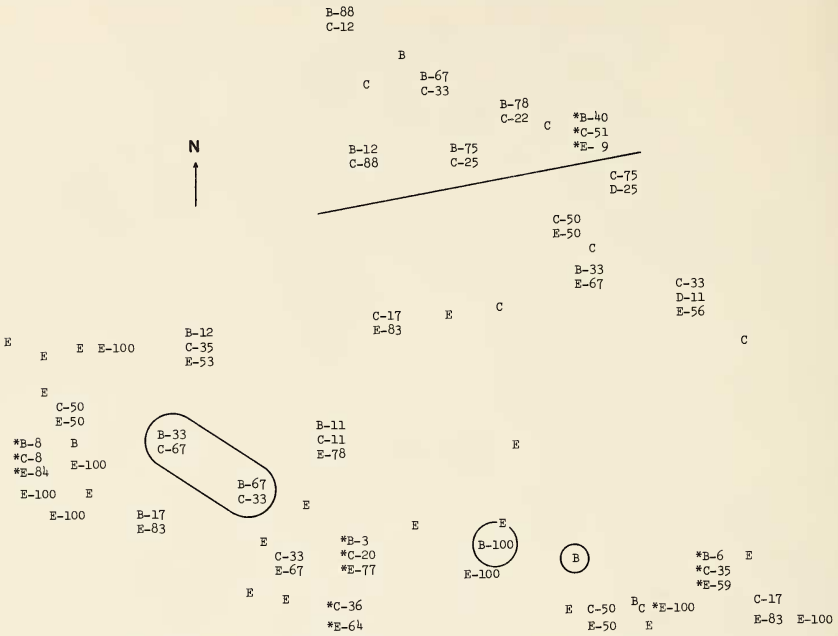

FIGURE 10. Relative geographic distribution of dorsal color pattern of form II individuals. Single letters indicate the state of a single specimen, letters followed by percentages indicate the distribution of states among 2 to 9 individuals, letters preceded by an asterisk and followed by percentages indicate the distribution of states among 10 or more individuals from a given region. See text for further explanation.

(Fig. 12A). All other populations have a preponderance of individuals lacking dorsolateral stripes (Fig. 11).

Mid-dorsal stripe—The clearest difference is between the populations from the Brasilian states of Minas Gerais, Rio de Janeiro, São Paulo and all other populations. No individuals from these three states have B or C category mid-dorsal stripes. The D category is also more abundant in populations from these three states than elsewhere (Fig. 13). Populations from the Brasilian territory of Amapá, French Guiana, Surinam, Guyana, and Venezuela do not have any individuals with E or G category stripes; category E or G individuals occur only in Amazonian populations (Fig. 13).

Toe tip development—Populations from Venezuela, the Brasilian state and territory of Acre and Rondônia, the mouth of the Amazon, and Belo Horizonte, Minas Gerais, Brasil differ from all other populations in having C category individuals (Fig. 14). Populations from the state of São Paulo, Brasil at Anhembi and Campos do Jordão are distinctive in having a preponderance of A category individuals (Fig. 14).

Discussion of Taxonomic Decisions

Combining the above distributions of character states, three transitional zones are apparent: 1) the mouth of the Amazon region, especially the Brasilian state of Amapá,

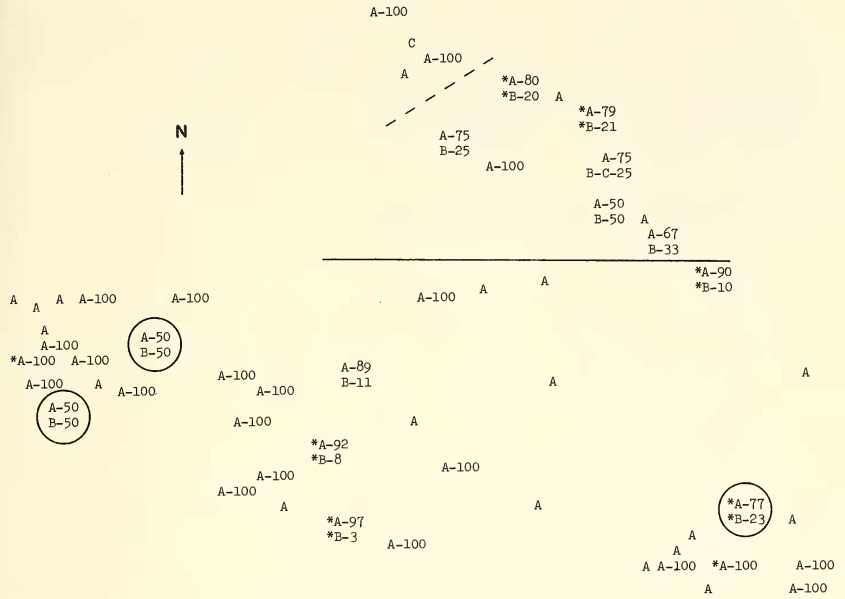

FIGURE 11. Relative geographic distribution of dorsolateral stripes of form II individuals. See legend of Fig. 10 and text for explanation.

separating the lands draining north from the Amazonian drainage; 2) a broad zone of western Brasil bordering Peru, Bolivia, and Paraguay; 3) the Brasilian states of Guanabara, Minas Gerais, Rio de Janeiro, and São Paulo.

Direct comparison of specimens from French Guiana, and the Brasilian territory and state of Amapá and Pará indicates that a single species is involved. Morphologically, the specimens are similar. There does appear to be a slight break in color pattern in the territory of Amapá, where the northern populations have many individuals with small spots on the dorsums, and the southern populations have individuals with larger, blotchier spots, or no distinct spots at all. I prefer not to recognize these differences taxonomically at present, because there are so few individuals available from the critical area of Amapá and the differences are not striking in the material at hand. The northern populations do differ from other populations with respect to details of dorsal pattern, dorsolateral stripes, and mid-dorsal stripes. These differences are here recognized in an informal manner (Fig. 24).

Direct comparison of individuals from the Brasilian territory of Rondônia, the states of Acre, Goiás, Mato Grosso, and from Bolivia do not indicate any clear cut differences. The situation, in fact, is rather confusing. The samples vary in degree of toe tip expansion, morphology, and dorsal pattern. Morphologically, the sample from Mato Grosso, Urucum, has an individual with a broader head (DZ 9204) than other individuals from the same sample. In other respects, the sample is uniform in characteristics. The single individual from Goiás, Jatai (WCAB 15139) has a more pointed

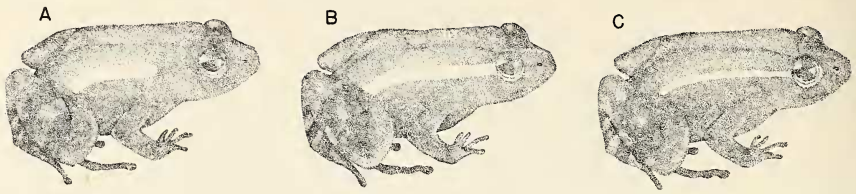

FIGURE 12. Category C dorsolateral stripes. A, form II specimen; B, form I specimen from greater Amazonia; C, form I specimen from southeast Brasil.

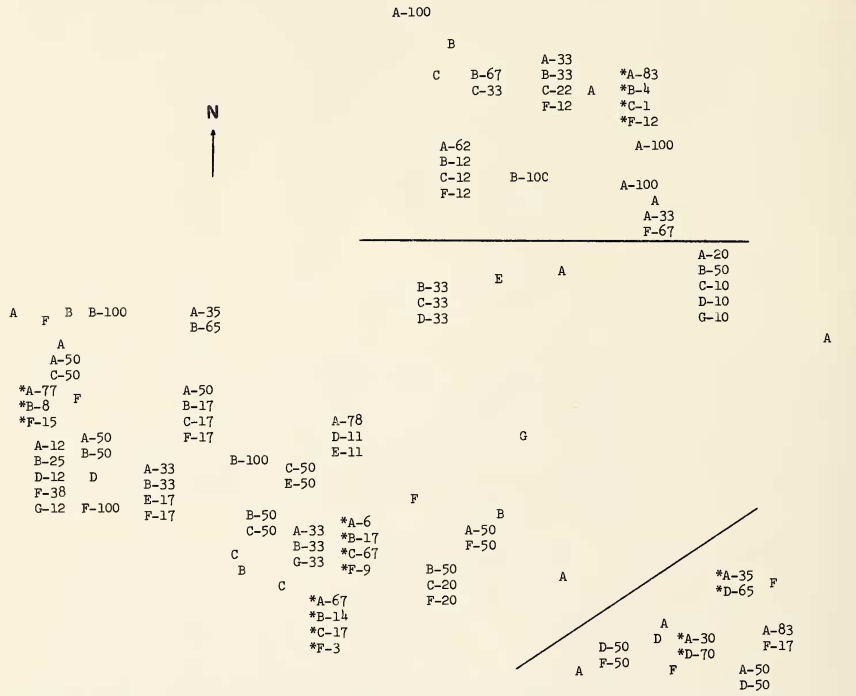

FIGURE 13. Relative geographic distribution of mid-dorsal stripes of form II individuals. See legend of Fig. 10 and text for explanation.

head than any of the other individuals. The single example from Vila Murtinho, Mato Grosso, next to Paraguay, has distinctive toe disks. The disks are not clearly of the I or II forms, that is rounded or flattened (Fig. 5). On the basis of the single faded specimen (UMMZ 76081), it is in fact difficult to tell whether it is a form I or II individual. The specimen is tentatively assigned to form II until fresh material has been collected. Pattern wise, the specimens from Tarauaca and Placido de Castro, Acre, Chapada dos Guimaraes, Mato Grosso, and Bolivia are similar in having individuals with small discrete dark spots more or less arranged in four longitudinal rows. The specimens from Feijó, Acre and the specimens from Urucum, Mato Grosso are similar in that some of the spots are coalesced along the mid-line to form short, narrow bands.

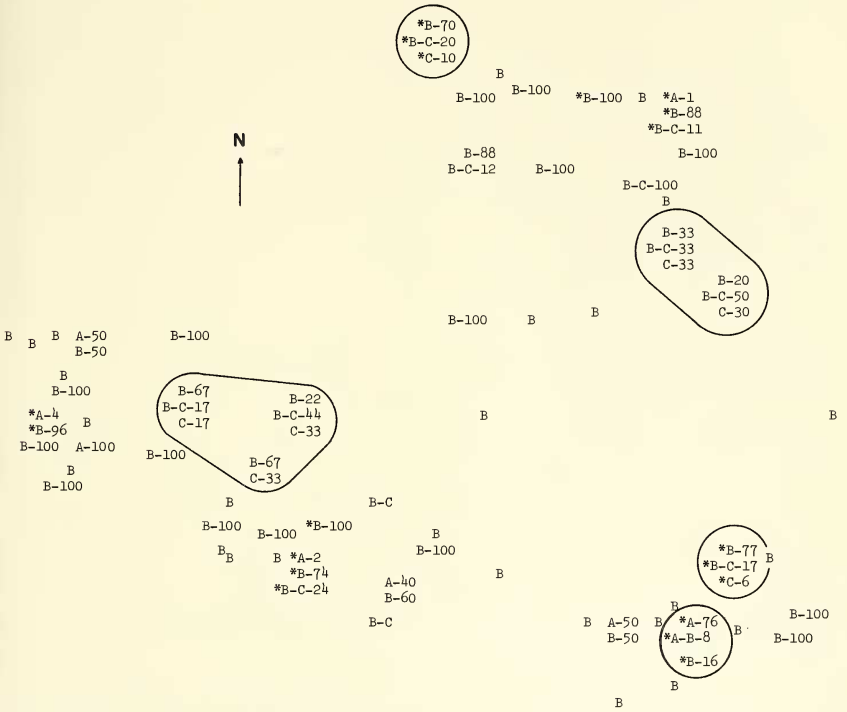

FIGURE 14. Relative geographic distribution of toe tip development of form II individuals. See legend of Fig. 10 and text for explanation.

The specimens from Jatai, Goiás and Sto. Antonio Leverger, Mato Grosso are similar in having many indistinct dark spots not arranged in any pattern. The specimens from Nhambiquara and Guajara-Assu Falls, Rondônia are too poorly preserved to determine the dorsal patterns. The overall pattern from this region is a mosaic. Few individuals are available from this region and there are no consistent, clear cut differences separating groups of populations. I prefer to treat informally the series of populations as distinctive until further work elucidates the relationships among these populations (Fig. 24). It should be kept in mind that the populations of frogs found along western Brasil are more or less distinctive from frogs of the northern Amazon, Peru, and Bolivia, but also, the individual populations within western Brasil are distinctive among themselves.

Direct comparison of individuals from the Brasilian states of Guanabara, Minas Gerais, Rio de Janeiro, São Paulo, Goiás, and Mato Grosso indicates that two distinctive types are represented. The specimens from Guanabara, Minas Gerais, Rio de Janeiro, and São Paulo differ from other specimens in that the appearance of many of the specimens is *Pseudis*-like, that is, with dorsally directed eyes and more or less triangular bodies. The mid-dorsal stripes are distinctive as noted above. Only two larval samples are known for any members of the Marmoratus group. Both belong to

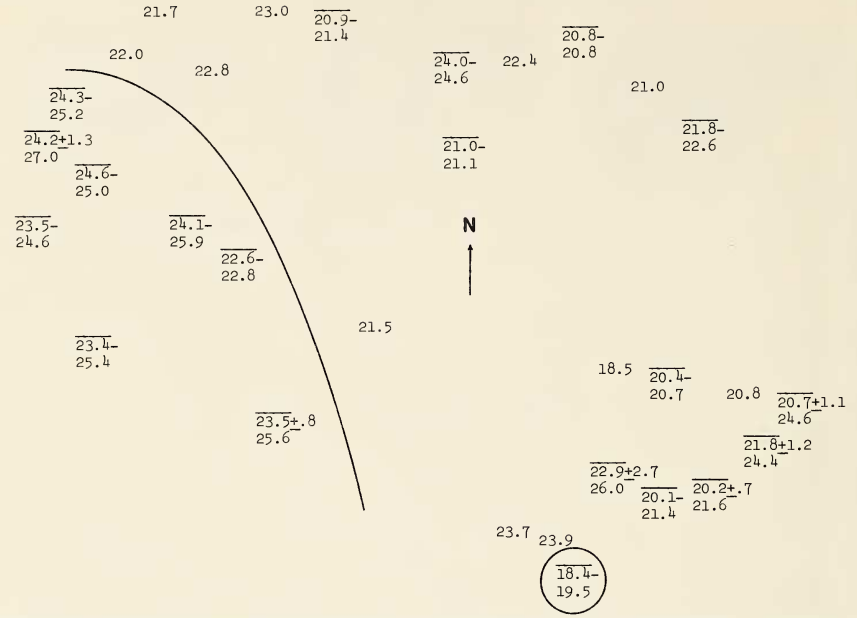

FIGURE 15. Relative geographic distribution of male size of form I individuals. See legend of Fig. 8 and text for explanation.

group II individuals. One sample is from French Guiana, Regina, the other from São Paulo, Campos do Jordão. The two tadpole lots are strikingly different. The larvae from Regina lack spiracles and denticles in the tooth rows (Fig. 25), whereas the larvae from Campos do Jordão have spiracles and well-developed denticulate tooth rows (Fig. 23). These differences are certainly indicative of species differences. Life history information may well clarify the status of the populations lying between the extremes of Regina and Campos do Jordão. I consider the form II populations from Minas Gerais, Rio de Janeiro, and São Paulo to represent a distinct species from all other form II populations (Fig. 24). Within the southeast coastal Brasilian species, the specimens from Belo Horizonte, Minas Gerais are the most distinctive. None of the individuals have distinct, small dark spots, many individuals are finely mottled, a pattern not seen elsewhere, and some individuals have C category disks.

Analysis of Form I Specimens

Male size—Form I males range in size from 16.2 to 27.0 mm. There are six samples with 10 or more males for which standard errors were calculated: one from Ecuador, one from Bolivia, and two each from the Brasilian states of Rio de Janeiro and São Paulo. The sample from around Teresópolis, Rio de Janeiro differs from the Ecuadorian and Bolivian samples by more than one standard error, the sample from Ilha São Sebastião also differs from the Ecuadorian and Bolivian samples by more than one standard error. None of the other samples differ significantly (Fig. 15). There is

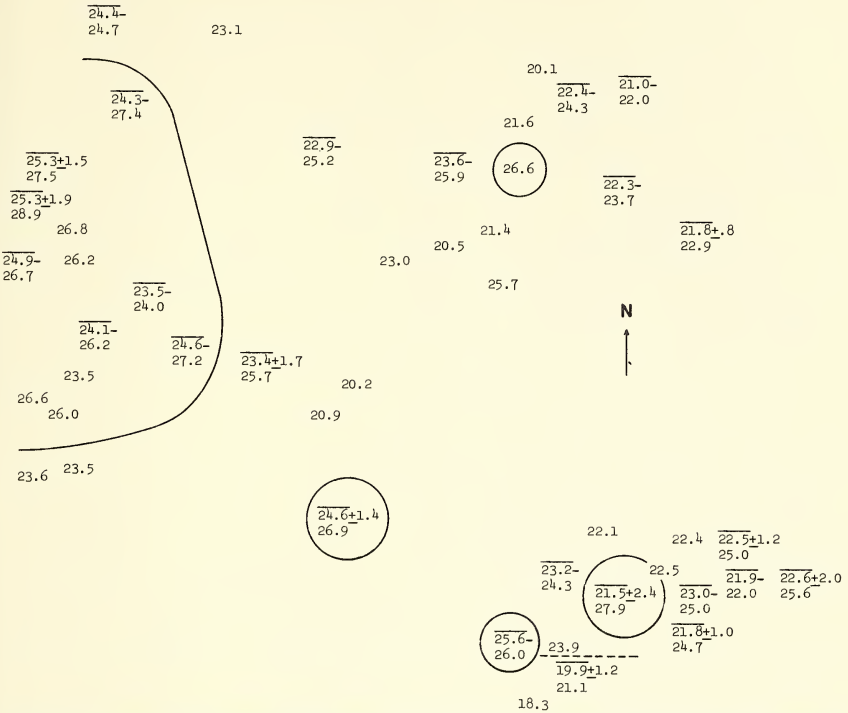

FIGURE 16. Relative geographic distribution of female size of form I individuals. See legend of Fig. 8 and text for explanation.

no distinctive geographic pattern in male size: the largest individuals are found in the western Amazon regions of Ecuador, Peru, Bolivia, and Brasil; the smallest individuals are from the state of Santa Catarina, Brasil (Fig. 15).

Female size—Form I females range in size from about 18 to 28.9 mm. Ten samples are represented by 10 or more individuals for which standard errors were determined: 1) Provincia de Napo, Ecuador, 2) Provincia de Pastaza, Ecuador, 3) vicinity of Benjamin Constant, Amazonas, Brasil, 4) vicinity of Belém, Pará, Brasil, 5) Buenavista, Santa Cruz, Bolivia, 6) vicinity of Teresopólis, Rio de Janeiro, Brasil, 7) vicinity of Rio de Janeiro, Guanabara, Brasil, 8) Ilha São Sebastião, São Paulo, Brasil, 9) vicinity of São Paulo, São Paulo, 10) Humboldt, Santa Catarina, Brasil. Sample 10 differs by more than one standard error from samples 1, 2, 3, 5, 6; sample 8 from samples 1, 2, 5; sample 4 from samples 1, 2, 5; sample 1 from sample 6. None of the other combinations differ significantly. No distinct patterns are evident in the geographic distribution of female size: the largest individuals (S–VL≥26.0 mm) are found in the western Amazonian regions of Colombia, Ecuador, and Peru, and the isolated localities of Sipaliwini, Nickerie, Surinam; Buenavista, Santa Cruz, Bolivia; Alcatrazes Is., São Paulo, Brasil; Pôrto de Cima, Morretes, Parana, Brasil; the smallest individuals are found in the state of Santa Catarina, Brasil (Fig. 16).

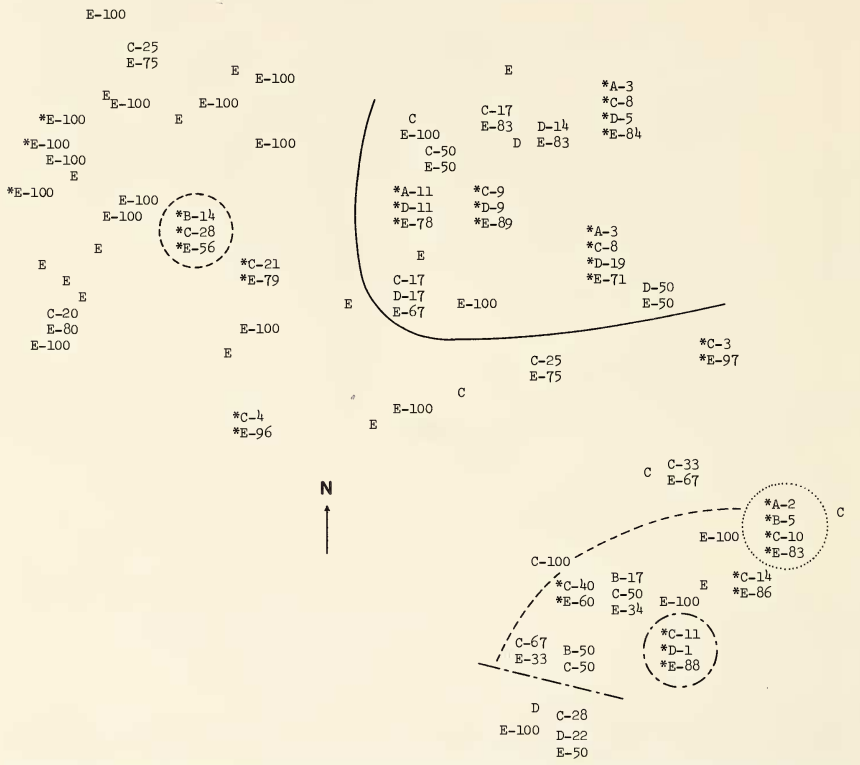

FIGURE 17. Relative geographic distribution of dorsal color pattern of form I individuals. See legend of Fig. 10 and text for explanation.

Male snout ratio—Six localities are represented by 10 or more males for which standard errors were determined on the snout ratios: 1) Provincia de Pastaza, Ecuador, .70 (mean) ± .06 (one standard error); 2) Buenavista, Santa Cruz, Bolivia, .72 ± .03; 3) vicinity of Teresópolis, Rio de Janeiro, Brasil, .71 ± .04; 4) vicinity of Rio de Janeiro, Guanabara, Brasil, .73 ± .04; 5) Ilha São Sebastião, São Paulo, Brasil, .68 ± .05; 6) vicinity of São Paulo, São Paulo, Brasil, .72 ± .04. No geographic patterns or trends were evident when the data were plotted on a map.

Female snout ratio—The female snout ratio is consistently smaller than the male snout ratio at any locality represented by at least two specimens of each sex. Ten samples are represented by 10 or more individuals for which standard errors were determined: 1) Provincia de Napo, Ecuador, .64 ± .06, 2) Provincia de Pastaza, Ecuador, .65 ± .05, 3) vicinity of Benjamin Constant, Amazonas, Brasil, .69 ± .07, 4) vicinity of Belém, Pará, Brasil, .65 ± .04, 5) Buenavista, Santa Cruz, Bolivia, .67 ± .04, 6) vicinity of Teresópolis, Rio de Janeiro, Brasil, .70 ± .04, 7) vicinity of Rio de Janeiro, Guanabara, Brasil, .69 ± .05, 8) Ilha São Sebastião, São Paulo, Brasil, .67 ± .04, 9) vicinity of São Paulo, São Paulo, Brasil, .67 ± .06, 10) Humboldt, Santa Catarina, Brasil, .73 ± .03. Sample 10 differs by 1 standard error or more from

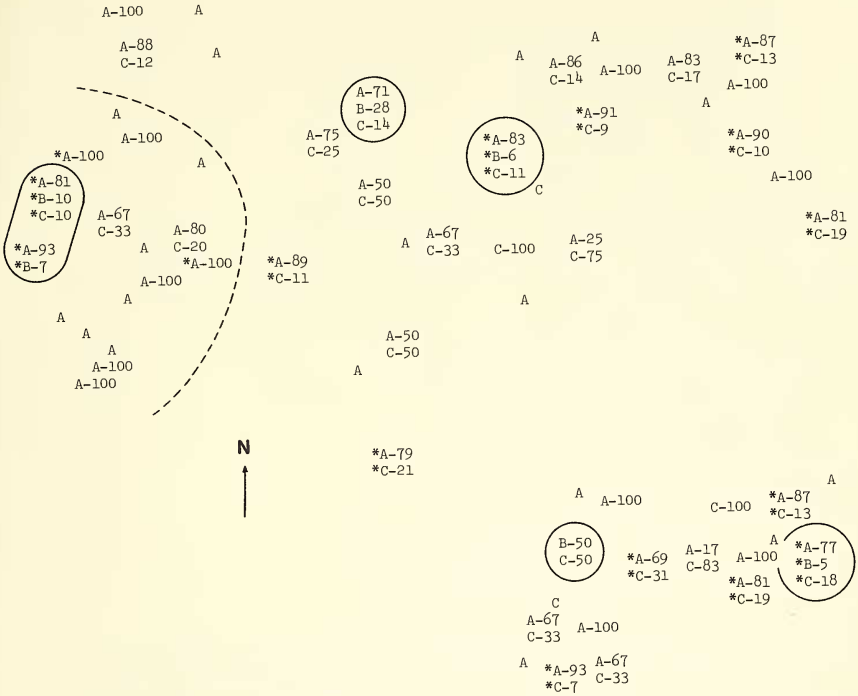

FIGURE 18. Relative geographic distribution of dorsolateral stripes of form I individuals. See legend of Fig. 10 and text for explanation.

samples 1, 2, and 4. Other than the samples of frogs from Humboldt having long snouts, no geographic trends were apparent when the ratios were plotted on a map.

Dorsal pattern—Most individuals are either C or E category with respect to their dorsal patterns. The B category is found in a few individuals from Estiron, Ampiacu River, Loreto, Peru, and in scattered populations in the Brasilian states of Rio de Janeiro, São Paulo, and Parana (Fig. 17). The A category is found in a low frequency in the northern populations and from around Teresópolis, Rio de Janeiro, Brasil (Fig. 17). The D category is found in low or moderate frequency in the northern populations, Ilha São Sebastião, São Paulo, Brasil, and the state of Santa Catarina, Brasil (Fig. 17).

Dorsolateral stripes—Most populations have around a 20% frequency of individuals with C category stripes (Fig. 18). The only populations in which the C category was absent in samples of 10 or more individuals are from the western Amazon regions of Ecuador and Peru (Fig. 18). Low frequencies of B category individuals are found in central and southern Amazonian Ecuador, southern Venezuela, southern Guyana, around Rio de Janeiro, Guanabara, Brasil, and Itapetininga, São Paulo, Brasil (Fig. 18).

Mid-dorsal stripe—Most samples have individuals with A, D, and F category

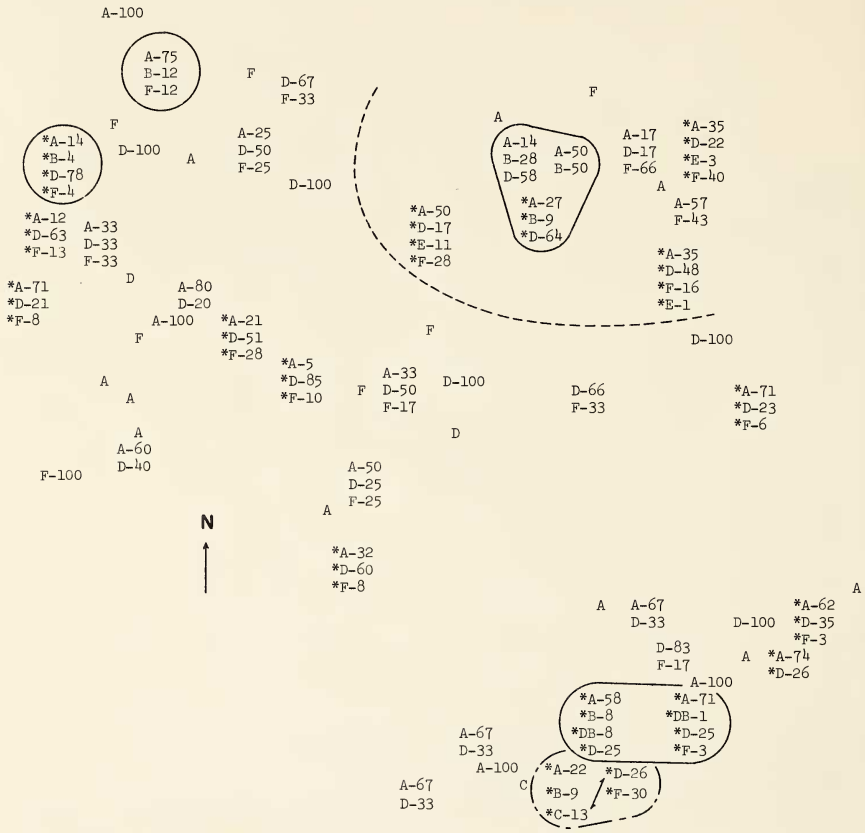

FIGURE 19. Relative geographic distribution of mid-dorsal stripes of form I individuals. See legend of Fig. 10 and text for explanation.

stripes (Fig. 19). B category stripes are found in low to moderate frequencies in samples from the southern border of Guyana and Surinam; Villavicencio, Meta, Colombia; Provincia de Napo, Ecuador; Ilha de São Sebastião, São Paulo, Brasil, around São Paulo, São Paulo, Brasil; and the state of Santa Catarina, Brasil (Fig. 19). The only C category individuals are from the state of Santa Catarina, Brasil; the only E category individuals are found in northcentral samples and are strictly correlated with the A category dorsal pattern (Fig. 19).

Toe tip development—During the data taking, it was noticed that juvenile specimens often had poorly differentiated disks while adults from the same locality had well-developed disks. Only adults were used for this character analysis. Almost all samples are characterized by having individuals with either C or D category disks. B category individuals are from three separate areas: Sipaliwini, Nickerie, Surinam; southern Venezuela; and the state of Parana, Brasil (Fig. 20). BC category individuals are from five areas: French Guiana and east-central Surinam; Abunã, Rondônia,

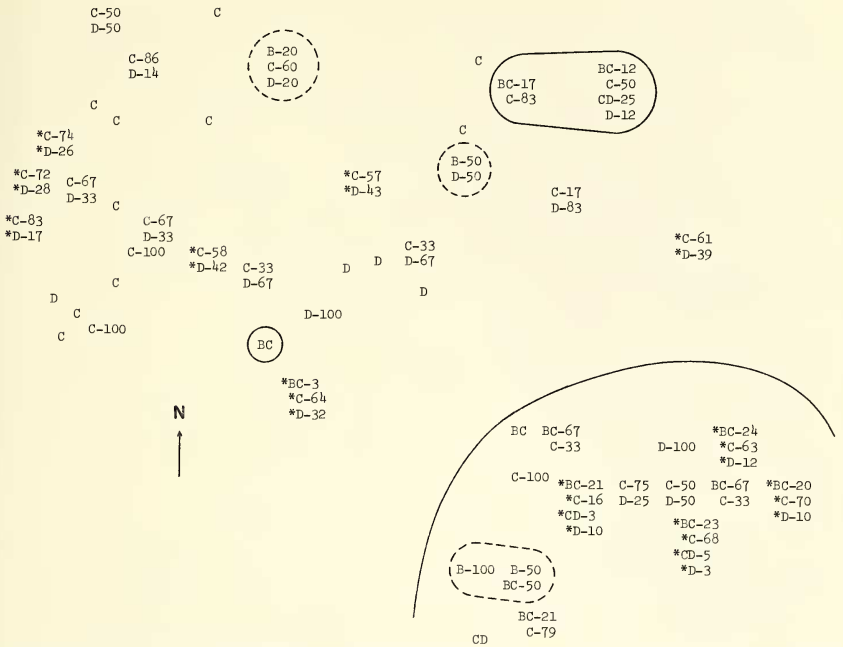

FIGURE 20. Relative geographic distribution of toe tip development of form I individuals. See legend of Fig. 10 and text for explanation.

Brasil; Buenavista, Santa Cruz, Bolivia; the states of Rio de Janeiro and São Paulo, Brasil; and the state of Santa Catarina, Brasil (Fig. 20).

Discussion of Taxonomic Decisions

The above analyses indicate that there are three somewhat distinctive regions: 1) the region represented by the north-central samples. The samples are uniform among themselves, but differ with respect to details of dorsal pattern, dorsolateral stripes, mid-dorsal stripes, and toe disk development from the other samples; 2) the region represented by the western Amazonian samples from Colombia, Ecuador, Peru, Amazonas, Brasil, and Bolivia. The samples are basically uniform among themselves, but differ with respect to details of size and dorsolateral stripes from the other samples; 3) the region of the Brasilian states of Rio de Janeiro, São Paulo, Parana, and Santa Catarina. These samples differ among themselves and collectively differ from the other samples.

The specimens from southern Guyana and Surinam are the most robust individuals of those examined (e.g., Fig. 4, form A). These individuals contrast in body shape with specimens from localities directly south along the Amazon River in the Brasilian states of Amazonas and Pará. There is a continuum of body shape of specimens from southern Guyana and southern Surinam→ western and northern Surinam and French Guiana→ Territorio de Amapá, Brasil→ Estados do Pará, Brasil and eastern

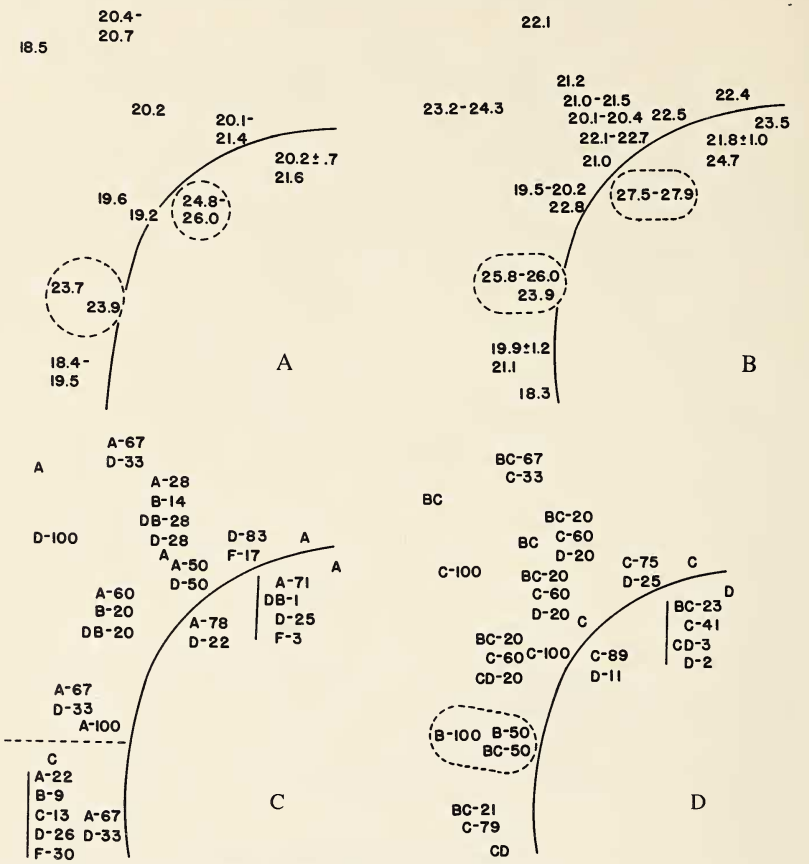

FIGURE 21. Relative geographic distribution of four characters of form I individuals in the Brasilian states of São Paulo, Parana, and Santa Catarina. To the left and above lines is mainland, figures to the right of lines indicate island populations. A, Male size–See legend of Fig. 8 and text for explanation. B, Female size–See legend of Fig. 8 and text for explanation. C, Mid-dorsal stripes–See legend of Fig. 10 except that vertical bar rather than asterisks indicates a sample size of 10 or more individuals. See text for further explanation. D, Toe tip development–As for mid-dorsal stripes.

Amazonas, Brasil, however. With the specimens at hand, and lack of large series from critical areas, I prefer not to recognize these differences as representative of specific differentiation. The north central specimens are distinctive in details of body shape, dorsal pattern, and toe disks, which features are recognized informally (Fig. 27).

The specimens from northern draining lands of Colombia and Venezuela are more similar to specimens from Amazonian Colombia, Ecuador, and Peru than the north-central South American localities. Specimens from western Amazonian Colombia, Brasil, Ecuador, Peru, and Bolivia are somewhat distinctive in details of size and dorsolateral stripes; these differences together with the homogeneity of dorsal pattern, mid-dorsal stripes, and toe disk development are recognized informally (Fig. 27).

All specimens from the Brasilian states of Rio de Janeiro, São Paulo, Parana, and Santa Catarina differ from other specimens in not being as robust, most of the specimens having dorsolateral stripes of narrower type (Fig. 12C), B and C category mid-dorsal stripes present, and B and BC category toe disks reasonably represented. While these differences are not absolute, they appear to be consistent. There is at present, a wide zone where no form I individuals have been collected, making it difficult to assess the degree of taxonomic differentiation of the southeast Brasil forms from the Amazonian and northern South American form. To my knowledge, no comparative information on either mating call structure or larvae is available. Taking the cue from the form II analysis and for reasons discussed in the relationship section, I prefer to recognize the differences at the species level.

There remains within the southeast Brasilian form I samples considerable heterogeneity, calling for a closer scrutiny of variation in the states of São Paulo, Parana, and Santa Catarina with respect to size, mid-dorsal stripes and toe disks.

The geographic distribution of male and female size is a continuum from relatively small size in northern São Paulo to the smallest sizes in Santa Catarina with three large-sized populations from Alcatrazes Island, São Paulo, and Parana (Fig. 21 A,B). The geographic distribution of mid-dorsal stripes is a crude continuum from B category in São Paulo, leading to expression of the B and C categories in Santa Catarina. The only real break is the unique presence of the C category in Santa Catarina (Fig. 21C). The geographic distribution of toe disks shows that the Parana samples are unique (Fig. 21D).

Taken together, the samples form an integrated series with the exception of the samples from Alcatrazes Island, São Paulo; Paranagua, Parana; and Pôrto de Cima, Morretes, Parana. The sample from Alcatrazes Island is unique only with respect to size, but in this respect it is distinctive. Gigantism is a relatively common phenomenon on islands, but neither of the island populations from São Sebastião nor Buzios are as distinctively large as the Alcatrazes population. Further work is needed to determine the significance of size in the Alcatrazes population. I consider the Alcatrazes population to represent the same species as the mainland form I species, but point out the distinctive large size of the population in an informal manner (Fig. 27). The samples from Paranagua and Pôrto de Cima, Morretes are distinctive with repect to size and toe disk development. The larger sizes of the specimens seem to be superimposed over the general trend of decreasing size of the mainland populations (Figs. 21 A,B); the B category of disk development is unique in these two samples. Data from three individuals from Volta Grande, Parana were not plotted on the maps as the specimens are faded juveniles. The 11.1 and 14.5 mm specimens have BC category disks, the 16.0 mm specimen has C category disks. These three individuals fit into the general patterns evidenced by the rest of the mainland form I individuals and contrast with the other individuals from Parana. As indicated previously, the decision to include the Paranagua and Pôrto de Cima, Morretes individuals in the form I individuals analysis was based on the fact that certain of these individuals had C category dorsolateral stripes. Direct comparison of the distinctive Parana specimens with form II specimens from São Paulo indicates that the only consistent difference is in the dorsolateral stripes. All specimens are of similar size, dorsal pattern, toe tip development, and

ventral pattern. I consider the Parana slender toed forms to represent the same species as the slender toed forms from São Paulo until further collections and information are gathered to indicate otherwise. The distinctiveness of the Parana form II individuals is pointed out in an informal manner, however (Fig. 24).

TAXONOMIC CONCLUSIONS

Five species are recognized. The most distinctive occurs in the arid interior of Brasil. The remaining four species form a complex of two allopatric groups of two species each. Two species are broadly sympatric over much of northern South America, Amazonia, and southwestern Brasil, the other two species are broadly sympatric over much of southeast Brasil from Minas Gerais to Santa Catarina.

NOMENCLATURE

Twelve names have been proposed previously for members of this group. In addition, one name has been associated with this group from time to time. Each of the names is dealt with in the order that it was proposed.

Rana pygmaea Spix, 1824. Dr. Günther Peters (personal communication) informed me that the type is no longer in the Berlin collections. W. Peters (1873) examined Spix's type material and briefly indicated that the holotype of *R. pygmaea* was from Bahia and that it was a juvenile of *Cystignathus pachypus*. *C. pachypus* has been placed in the synonymy of several species by various authors, but has most commonly been placed in the synonymy of *L. ocellatus*. Melin (1941: 60) suggested that *R. pygmaea* may actually pertain to members of the Marmoratus group. Examination of Spix's figure of *R. pygmaea* could support Melin's suggestion, although the figure is quite stylized. As the type is no longer extant, a decision must be made with the available data, the three most critical bits being the locality, the original figure, and W. Peter's synonymy based on examination of the specimen. No recent collections of members of the Marmoratus group are from the Brasilian state of Bahia. This, together with W. Peter's synonymy lead to the conclusion that the name does not apply to any member of the Marmoratus group but that the name applies to a member of either the Fuscus or Ocellatus groups.

Adenomera marmorata Fitzinger *in* Steindachner, 1867. There is confusion as to exactly who authored the species. In the text of Steindachner (1867), the new genus and species is clearly attributed to Fitzinger (p. 37). The proper citation would thus appear to be Fitzinger *in* Steindachner. As Parker (1932) points out, however, the description does not apply to the figure. Parker suggested that 1) a mix-up of specimens occurred and that the specimen that Steindachner chose to have illustrated was not the one described by Fitzinger, and 2) that the name *A. marmorata* be associated with the figure and the extant specimen rather than the description. As it is clear that Steindachner considered Fitzinger to be the author of *Adenomera marmorata* and apparently made a mistake in having the incorrect specimen figured, I prefer to use the citation *Adenomera marmorata* Fitzinger *in* Steindachner. The holotype (the figured specimen), Vienna 16453, is completely faded, but otherwise in good condition. I follow Bokermann's (1966) suggestion that the holotype originated from around Rio

de Janeiro, Brasil. The toe tips are expanded into distinct, flattened disks. *Adenomera marmorata* is the oldest available name for the form I species of southeast Brasil.

Cystignathus hylaedactylus Cope, 1868. The holotype, ANSP 2240, is presently in a state of fair preservation. The original description was extremely brief with respect to color pattern and no distinctive pattern can now be discerned on the type. Cope indicated that the toes had "distinct dilations at the end." Several of the toe tips of the holotype have been dissected by previous workers to examine the state of the terminal phalanges. The intact toe tips are somewhat desiccated, but are dilated. They correspond to the B–C state used herein. The swellings are rounded, not flattened. *Cystignathus hylaedactylus* Cope is the oldest available name for the form II species found in northern South America, Amazonia, and southwest Brasil.

Leptodactylus diptyx Boettger, 1885. One of the five syntypes, BMNH 1947.2.17.47, is clearly representative of the form II species from northern South America, Amazonia, and southwest Brasil. The tips of the toes are pointed, the dorsum is spotted, there are narrow lateral stripes on the sides of the body, and there is a mid-dorsal pin stripe from above the vent extending beyond the sacral region. I hereby designate BMNH 1947.2.17.47, an adult male, the lectotype of *Leptodactylus diptyx* Boettger. The locality of Paraguay represents the only record of any representative of the Marmoratus group from that country. Records are available close to the Paraguayan border in the state of Mato Grosso, Brasil, suggesing that the provenance of the type poses no problem.

Leptodactylus glandulosus Cope, 1887. Cope indicated that the species was small, it appears as though all of the 14 specimens comprising the type series are juveniles. The toe tips are either the A or B category, some individuals have the dorsum with indistinct spots, and some individuals have a light, mid-dorsal pin stripe from above the vent extending to the snout. *Leptodactylus glandulosus* clearly applies to the form II species from northern South America, Amazonia, and southwest Brasil. I hereby designate ANSP 10275 as the lectotype of *Leptodactylus glandulosus* Cope.

Leptodactylus hololius Boulenger, 1918. The holotype is in a good state of preservation. In addition to the spots on the anterior part of the head and body dorsally as described by Boulenger, indistinct spots are present more posteriorly. The tips of the toes are slightly expanded, state B., and rounded. The holotype is clearly representative of the form II species from northern South America, Amazonia, and southwest Brasil.

Leptodactylus nanus Müller, 1922. Dr. U. Gruber kindly sent the available type specimens. He informed me (personal communication) that the holotype, Munich 659/1920 was lost in the war. The three extant types are in excellent condition, with expanded toe disks and type C dorsolateral stripes. The types are clearly representative of the form I species of southeast Brasil, in particular the southern populations. I hereby designate the 19.4 mm S–VL female specimen, Munich 661/1920 as the lectotype of *Leptodactylus nanus* Müller.

Leptodactylus andreae Müller, 1923. The holotype, Munich 136/1911, was lost in the war (U. Gruber, personal communication). The remaining four types are in a good state of preservation. The types have expanded toe disks (type D), and one has category D dorsal pattern. The 21.1 mm S–VL specimen, Munich 145/1911, is hereby

designated as the lectotype of *Leptodactylus andreae* Müller (the specimen was not dissected, but apparently is a juvenile female). *Leptodactylus andreae* is the oldest available name for the form I species of northern South America including Amazonia.

Leptodactylus minutus Noble, 1923. The holotype is in a good state of preservation. The dorsum is spotted, there is a C category mid-dorsal stripe, and the toes are B category, all of which associate the holotype with the form II species from northern South America, Amazonia, and southwest Brasil.

Leptodactylus trivittatus Lutz, 1926. A series of syntypes at the United States National Museum are in fair to poor states of preservation. Only one of the specimens, a juvenile, has the pattern on which the name was based. For this reason, USNM 96943, a juvenile, is hereby designated as the lectotype of the species. The toe disks are C–D category and flattened. The name applies to the form I species of southeast Brasil.

Leptodactylus rugosus Melin, 1941. Lutz and Kloss (1952) pointed out that *L. rugosus* Melin was preoccupied by *L. rugosus* Noble and renamed Melin's species as *L. melini*. The holotype has category B toe tips which are rounded. The dorsal pattern is faded but may have been spotted. The sides are warty (as are many individuals of this group) and apparently this is the reason for the original specific name. The dorsum is smooth. The name clearly applies to the form II species of northern South America, Amazonia, and southwest Brasil.

Leptodactylus poeppigi Melin, 1941. The toe tips are B category, the dorsum has irregular spots and a B category mid-dorsal light pin stripe, all of which indicates the name applies to the form II species of northern South America, Amazonia, and southwest Brazil.

Leptodactylus martinezi Bokermann, 1956. The types were included in the analysis and were part of the form III species of central Brasil.

In summary, the form I species of southeast Brasil has been described three times, *A. marmorata* is the oldest name. The form I species of northern South America and Amazonia has been described once as *L. andreae*. The form II species of northern South America, Amazonia, and southwest Brasil has been described seven times, *C. hylaedactylus* is the oldest name. The form III species has been described once as *L. martinezi*. One species remains, which apparently has never been described. This new species is described in the next section.

Species Accounts

The information from the previous analyses is summarized in the accounts. Additional information was taken from a series of 10 males and 10 females of each species representing the extremes of geographic range within each species except for *L. martinezi,* for which all available adult specimens were examined. The snout-vent length and percentages of S–VL are mean values which are followed by one standard error except for male *L. martinezi*. The methods are the same as those used previously (Heyer, 1970b).

Adult members of the Melanonotus and Ocellatus species groups have distinct lateral fringes distinguishing them from members of the Marmoratus group which have free toes. Adult members of the Pentadactylus species group are moderate to large

sized frogs (greater than 60 mm S–VL), the males have thumb spines, differentiating them from the small sized (smaller than 31 mm S–VL) members of the Marmoratus group in which the males lack thumb spines. Members of the Marmoratus group can be differentiated from members of the Fuscus group as follows (characteristics for members of the Marmoratus group in parentheses): dorsolateral folds usually present (almost always absent), a light longitudinal stripe often on posterior face of thigh (absent), first finger usually much longer than second (about equal), moderate in size, 25–65 mm S–VL (small, never exceeding 31 mm S–VL).

Leptodactylus andreae Müller

Leptodactylus andreae Müller, 1923:41–43 (Type locality, Brasil: Para; Peixeboi. Lectotype Zool. Sammlung Bayr. Staates, hert. nr. 145/1911, juvenile female).

Diagnosis—The only other species in the Marmoratus species group in addition to *L. andreae* with flattened toe disks is *L. marmoratus*. Some individuals of *L. andreae* have a striped pattern dorsally, no *L. marmoratus* have dorsal longitudinal stripes, almost no *L. andreae* have a light mid-dorsal pin stripe extending from above the vent to beyond the sacral region, some *L. marmoratus* have such stripes extending to the shoulder region or to the snout.

Summary of characteristics—Adults: Dorsal outline of snout rounded, subovoid, or subelliptical in females, subovoid, subelliptical, or pointed in males; snout rounded in profile in females, rounded or usually rounded-acute in males; female snout ratio .643 ± .060, male snout ratio .703 ± .056, canthus rostralis indistinct; loreal slightly concave or obtuse in cross section; tympanum distinct, equal to or just greater than ½ diameter of eye; vocal sac single, internal or very slight folds under angle of jaw to forearm; vomerine teeth in transverse (usually) or very slightly obtuse series posterior to choanae; head length 38.8 ± 1.8% S–VL; head width narrower than length, 35.4 ± 1.9% S–VL; interorbital distance 9.1 ± 0.8% S–VL; length of first finger equal to, just greater than, or just lesser than length of second finger; dorsum smooth or with ridges, warts, or rarely tuberculate dorsolateral folds, males usually with white-tipped tubercles scattered over posterior dorsum, females almost always lacking such tubercles; no distinctive glands or two small round glands on either side of anus on hindlimb; toes usually with distinct, flattened disks (Figs. 1, C, D; 5, A); toes free; subarticular tubercles pronounced; no metatarsal fold; weak, sinuous tarsal fold extending ½–⅗ length of tarsus, usually smooth or with series of white-tipped tubercles; lower surface of tarsus and sole of foot almost smooth to profused with white-tipped tubercles; female size 24.1 ± 2.0 mm S–VL, 28.9 mm maximum, male size 23.3 ± 1.5 mm S–VL, 27.0 mm maximum; femur 42.1 ± 3.8% S–VL; tibia equal to or longer than femur, 45.8 ± 1.9% S–VL; foot longer than femur, equal to or longer than tibia, 48.2 ± 2.4% S–VL; dorsal pattern most commonly uniform (Fig. 2E), or often with indistinct marks (Fig. 2C) or distinct blotches (Fig. 2D), rarely with distinct lines (Fig. 2A), most individuals lacking light dorsolateral stripes, a few with narrow stripes, several with well defined light stripes from eye to groin (Fig. 12B), narrow light mid-dorsal stripe absent or extending from anus to sacral region or rarely to middle of back, broad mid-dorsal stripe from snout to anus present only in the individuals with striped dorsums (Fig. 2A), center of throat and belly immaculate, ventral

borders of chin, thigh, and tibia (or entire tibia) mottled, some males with dark vocal folds; posterior thigh finely mottled to uniform.

Geographic variation—Populations from northern South America (Guyana, Surinam, French Guiana and part of Amapá, Brasil) are rather uniform with respect to morphology and color pattern. They differ in detail from all other populations in having the dorsal pattern of three light broad longitudinal stripes (A category) represented at a low frequency, the blotched dorsal pattern represented in moderate frequency, a low frequency of narrow dorsolateral stripes not reaching the eye (category B), and the pin stripe mid-dorsal stripe (B category) is present at a low frequency. Populations from the western Amazon (Colombia, Ecuador, Peru, Amazonas-Brasil, Bolivia) are also rather uniform with respect to morphology and color pattern. They differ in detail from other populations in being larger and having a very low frequency of broad light dorsolateral stripes (C category). Remaining populations do not demonstrate any geographic trends in morphology or color pattern.

Distribution (Fig. 27)—Range: North, central, and westen South America east of the Andes. Known elevational range, sea level to 1200 m.

Localities—BOLIVIA. *Santa Cruz:* Buenavista, 500 m, MCZ 15583, UMMZ 64031 B–C, J, 64032B 66483A–F, 66484A–E, 66493A–D, F, 66494C, 66504A–G, 66542, 66611.

BRASIL. *Amapá:* Mazagão, WCAB 19184-5; Serra do Navio, LACM 44281, 44726-53, WCAB 2317-8, 3623, 18169, 18224, 19979, 35245-8. *Amazonas:* Codajáz, DZ 28325; Ducke reserve, near Manaus, KU 129938-41; Ilha Terra Nova, in Amazon River, LACM 44714, 44716; Itapiranga, DZ 27755, 27757-8; Lago de January, island next to Channel Pixuna, LACM 44719, 44721-3; Livramento, region, AMNH 44782-6; Tapuruquara, WCAB 8768-9; Teresina, 3 hrs downstream Leticia, LACM 50179-97. *Pará:* Belém, 20 m, DZ 24999-25000, LACM 44792-8, USNM 154062-65; IPEAN, 3 km E Belém, KU 127338, 127340-52, 127354-5, 12357, 127359-64, 127366-9, 127371-5, 127377, 127380-90, 127392-4, 128268-71; Jacareacanga, DZ 24949, WCAB 45483, 45508-12; Rio Mapuera (at equator), 80 m, AMNH 80026; Sudam Floral Reserve, 74 km SE Santarem, KU 129934-7. *Rondônia:* Abuña, WCAB 10050; Igarapé Marmelo, WCAB 9852, 9856, 9858; Pôrto Velho and vicinity, UMMZ 64119A–C, E.

COLOMBIA. *Amazonas:* Río Apaporis, USNM 144843. *Caqueta:* Tres Esquinas, Río Arteguaza, WCAB 40641-3; Villa Maria, USNM 147038. *Cordoba;* Tierra Alta, FMNH 61802, 61805. *Meta;* Villavicencio, 500 m, FMNH 30812, 81795-8, USNM 144844-6. *Vichada;* Anabén, UPR 102.

ECUADOR. *Moruna-Santiago:* trail between Copal and Mendez, 580-910 m, USNM 192705; trail between Plan Grande and Rosario, between Mendez and Limon (Gral. Plaza), 910-1130 m, USNM 192706-9; Sucua and environs, 820 m, USNM 192692-9; Río Yuquipa, nr. Macas, USNM 192710. *Napo:* Lago Agrio, KU 126243-5; Loreto, 400 m, JAP 9216; Puerto Libre, Río Aguarico, 570 m, KU 119355–86; 2 km W Puerto Napo, Hacienda of George Kiederle, on S bank of Rio Napo, 470 m, USNM 192703; San José Viejo de Sumaco, JAP 9215; Santa Caecilia, 340 m, KU 109161-2, 111426-8, 119344-5, 119348-9, 119352-4 UMMZ 129285(2); 1 mi NE Tena, E of Río Masahualli, 490 m, USNM 192701-2. *Pastaza:* Arajuno, 537

m, USNM 192712-25; Canelos, 530 m, KU 119324-42; Caveceras del Río Bobonaza, 670 m, USNM 192685-6, 192689-91; 2½ km downstream from Caveceras, 650 m, USNM 192687-8; Moreta, below Montalvo, Río Bobonaza, JAP 9219, 3 km SSE Puyo, 975 m, USNM 192683-4; 5 km SSE Puyo, Hacienda Madrid, 975 m, USNM 192681-2; Headwaters of Río Capahuari, JAP 9209-10; Río Conambo, JAP 9220-1; Río Pindo, 190 m, USNM 192726; Río Puyo at Puyo, 970 m, USNM 192680; Río Rutuno, trib. of Río Bobanaza, JAP 9214; Río Sandalias, trib. of Río Puyo, Río Bobonaza, USNM 192711, WCAB 35526-7; Río Solis, headwaters of Río Bobonaza, JAP 9211-2; Río Villano, 300–400 m, GOV 9523, JAP 9213, 9217; 2 km S. Shell Mera, 970 m, USNM 192700; Veracruz (± 10 km E Puyo), 1000 m, KU 119323, USNM 192704.

FRENCH GUIANA. Cabassou (Rémire), LG 358-9; 6 km SSE Cayenne, Mont. Cabassou, LACM 44592; trail between Flueve Approuague and summit Mont Tortue, LACM 44607-11; Maturi, LG 555-6; Montagne des Chevaux, LG 397-8; Regina, 25 m, LACM 44597-9, 44612-6; Rémire, LG 789; Lower Rivière Matarony, upstream from Matarony, LACM 44593-6, 44600-5, 44617-23; Rochambeau, LG 711, 724, 733, 741-5; Sant Tortue, Orstom Camp, LACM 44606, 44669; trail from Sophie to La Greve, MCZ 44559.

GUYANA. *Essequibo:* N of Acarahy Mts W of New River, KU 69714; Shudikar-wan, 200-300 m, AMNH 46264, 87877-85, 46268-9, 46272-3, 80028, 87886-8.

PERU. *Loreto:* Estiron, Ampiacu River, 200 m, DZ 24284-90, 24838-41, 24843, 24847, 25491; Iparia, MCZ 75033, 75035-8; Iquitos, AMNH 43471; Itaya River, 150 m, AMNH 42175; Lago Mirano, mouth of Río Napo (at Río Amazonas), AMNH 43155, 43161, 43168, 43184, 43190; Pampa Hermosa (Cushabatay), 176 m, AMNH 42048; Río Tamaya, 150 m, AMNH 43363, 43423-4; Tibi Playa (above mo. Rio Ucayali), 150 m, AMNH 42785; *Pasco;* Iscozazin Valley, Pan de Azucar, 380 m, LACM 40654, 40657; San Martín; Achinamisa, below Chasuta on Río Huallaga, AMNH 42595.

SURINAM. *Marowijne:* Anapaike Village, Lawa River, DZ 24778-80; Lawa River; DZ 24774-6. *Nickerie:* Kaysergebergte, RM 16751(2); Post Gonini, Coeroeni Rivier, RM 16739(2), 16740(4); Post Tigrie, New Rivier, RM 16741; Sipaliwini, RM 16724, 16727, 16745, 16749(7), 16753. *Suriname:* Berlijn, RM 16742.

VENEZUELA. *Amazonas:* Base of Mt. Duida, UPR 3125-9; Pico Cunoto, Mt. Duida, UPR 3130; Mt. Marahuaca, 1200 m, UPR 103. *Barinas:* Palma Sola, UMMZ 55550.

Leptodactylus bokermanni, new species

Figures 22, 23

Holotype—UMMZ 104257, an adult male from Paranaguá, Estado do Parana, Brasil. Elevation 30 m.

Paratopotype—WCAB 22787.

Paratypes—BRASIL. *Minas Gerais;* Agua Limpa, USNM 96997; Belo Horizonte, UMMZ 109990 (2 specimens), WCAB 7236-42; Poços de Caldas, 1000 m, WCAB 18735; Serra da Piedade, Caeté, DZ 25071. *Parana:* Pôrto de Cima, Morretes,

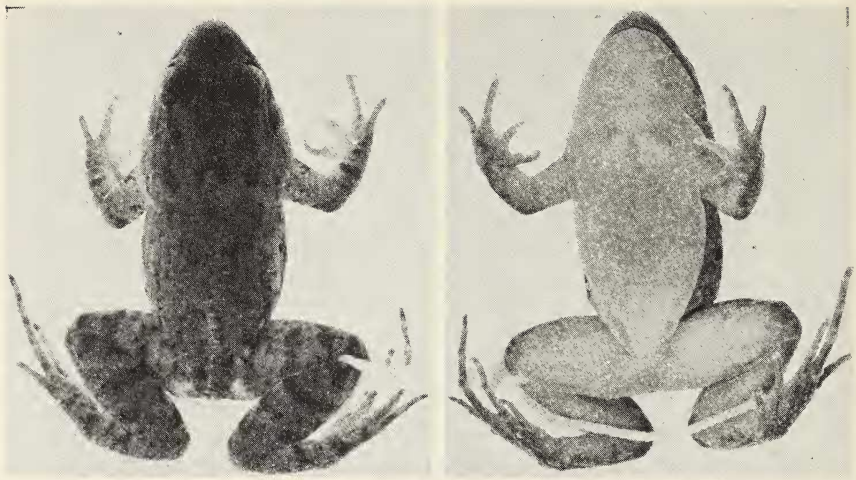

FIGURE 22. Dorsal and ventral views of a paratype of *Leptodactylus bokermanni,* WCAB 30035, from Campos do Jordão, São Paulo, Brasil. Specimen is 24.3 mm S–VL.

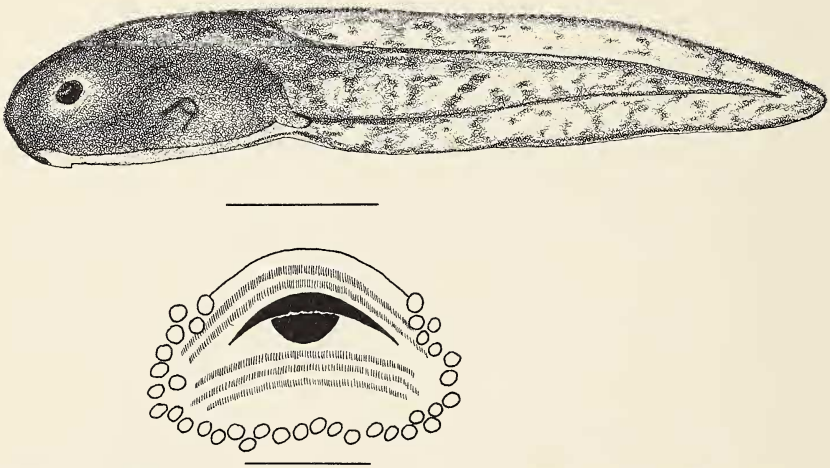

FIGURE 23. Lateral view and mouthparts of larva of *Leptodactylus bokermanni.* Upper line equals 1 cm, lower line equals 1 mm.

DZ 15781-2, 24292. *Rio de Janeiro:* Niteroí, AMNH 20278, 87876; Saco São Fracisco, USNM 99122; Teresópolis, Guapi, USNM 97681, 97683-90. *São Paulo:* Anhembi, 400 m, WCAB 30860-1; Botucatu, DZ 6388; Campos do Jordão, WCAB 30035, 30097-102, 34462 (larvae), 34463-76, 36957-60, 37628-9; Iguape, DZ 508; Limeira, DZ 9638; Piquete, DZ 530; Sta. Branca, DZ 25445.

Diagnosis—The other species of the Marmoratus group in addition to *L. bokermanni* with toe tips not developed into flattened disks are *L. hylaedactylus* and *L.*

martinezi. *Leptodactylus bokermanni* does not have four longitudinal rows of symmetric dark spots as does *L. martinezi*. No individuals of *L. bokermanni* have a light mid-dorsal stripe extending from above the vent to the middle of the body or to the snout, many *L. hylaedactylus* do; *L. bokermanni* larvae have a spiracle and well-developed denticle rows, *L. hylaedactylus* larvae lack a spiracle and denticle rows.

Description of Holotype—Dorsal outline of snout subelliptical; snout profile rounded; canthus rostralis indistinct; loreal slightly concave in cross section; tympanum distinct, greatest diameter ½ eye diameter; vomerine teeth in short transverse series, posterior to choanae; vocal slits elongate, paired; vocal sac single, vocal fold from jaw to forearm on each side; finger lengths in order of decreasing size III>II>I>IV, first finger just shorter than second; large ovoid inner metacarpal tubercle smaller than ovoid outer metacarpal tubercle; head and shoulders smooth, sacral region and upper surfaces of tibia profused with white-tipped tubercles; angle of jaw and sides with diffuse glandular development, compact, white oval glands on either side of the anus on hind limbs; glandular fold from eye, over tympanum, to shoulder; ventral surfaces smooth, belly fold distinct; toe tips slightly expanded, state B; toes without fringe; subarticular tubercles moderately developed; distinct, oval inner metatarsal tubercle larger than rounded, distinct outer metatarsal tubercle; tarsal fold not continuous with inner metatarsal tubercle, extending ⅞ distance of tarsus; line of white-tipped tubercles in place of metatarsal fold; lower surface of tarsus and sole of foot profused with white-tipped tubercles.

Snout-vent, 24.0 mm; head length, 9.0 mm; head width 7.9 mm; interorbital distance, 2.2 mm; greatest diameter of tympanum, 1.3 mm; diameter of eye, 2.7 mm; eye-nostril distance, 2.0 mm; femur, 9.7 mm; tibia, 10.4 mm; foot, 12.3 mm.

Dorsum cream, in preservative (probably faded), with tan markings, interorbital bar extended into a triangle posteriorly, posterior tip of interorbital triangle contiguous with a chevron in shoulder region, dorsolateral dark stripes from shoulder to groin, other tan markings in sacral region; upper surfaces of limbs striped, supratympanic fold dark; throat profused with melanophores, other ventral surfaces appearing immaculate; posterior surface of thigh mottled.

Summary of characteristics—Adults: Dorsal outline of snout rounded, subovoid, or subelliptical in females, subovoid, subelliptical, or pointed in males; snout profile rounded in females, rounded or rounded-acute in males; female snout ratio .702 ± .046, male snout ratio .717 ± .050; canthus rostralis indistinct; loreal very slightly concave or obtuse in cross section; tympanum distinct, greatest diameter equal to or just greater than ½ eye diameter; male vocal slits elongate, very slightly oblique to jaw or parallel to jaw; vocal sac single, internal or a slight fold along margin of jaw to forearm; vomerine teeth in transverse series, posterior to choanae; head length 38.2 ± 1.7% S–VL; head width less than length, 34.0 ± 1.4% S–VL; interorbital distance 8.9 ± 0.8% S–VL; length of first finger equal to or just greater than length of second finger; dorsum smooth or with ridges or warts, males often with white-tipped tubercles posteriorly, females rarely with white-tipped tubercles posteriorly, sometimes appearing glandular over much of body, with no distinct glands or some males with distinct, small, ovoid glands on either side of anus on hindlimb; toes commonly pointed or slightly swollen at tips (Fig. 1A, B), but when disked, disks rounded, never flattened

FIGURE 24. Distribution of *Leptodactylus bokermanni* (triangles) and *L. hylaedactylus* (circles). Solid circles indicate 1) a northern homogeneous population and 2) distinctive heterogeneous grouping of localities. Open triangles indicate distinctive southern populations of *L. bokermanni*. See text for further details.

(Fig. 5B); toes free; subarticular tubercles moderately developed; line of tubercles forming a metatarsal fold or absent; weak, sinuous or almost straight, tuberculate, tarsal fold extending ⅜ to ¾ length of tarsus; lower tarsus and sole of foot scattered or profused with white tipped tubercles; female size 24.2 ± 2.5 mm S–VL, 27.6 mm maximum, male size 23.2 ± 1.2 mm S–VL, 25.1 mm maximum; femur 41.0 ± 2.6% S–VL; tibia equal to or longer than femur, 44.0 ± 1.7% S–VL; foot longer than femur or tibia, 50.2 ± 2.1% S–VL; dorsal pattern commonly uniform (Fig. 2E) or with indistinct marks (Fig. 2C), rarely with distinct spots (Fig. 2B), most individuals lacking dorsolateral stripes, rare individuals with narrow or broad light stripes from eye to groin, narrow, light mid-dorsal stripe from anus not extending past sacral region or absent; venter immaculate or scattered with melanophores, not distinctly mottled; posterior face of thigh mottled to uniform.

Larvae: Nostril nearer tip of snout than eye; distance between nares about equal to or just less than interorbital distance; eye moderate, 10.5 ± 1.2% body length; mouthparts subterminal; oral papillae in single row; oral disk entire; oral disk width 27.0 ± 1.8% body length; anterior oral papilla gap 77.8 ± 6.6% oral disk width; tooth row formula $\frac{2}{1\text{-}1}$ or $\frac{2}{3}$, denticles in posteriormost row weakly or not developed; beak moderately developed, spiracle sinistral, halfway up body, ⅜ distance from tip of snout to anus; dorsal fin origin at body-tail juncture; tail height just greater than body height; tail tip elongate, rounded to pointed; anal tube median; dorsum dark, uniform gray to brown, in preservative; venter with profusion of melanophores on throat region, no melanophores on belly or anal tube; few or no melanophores on ventral tail fin, rest of tail mottled; total length largest specimen, stage 30, 13.5 mm; body length 31.4 ± 1.0% total length.

Geographic variation—Specimens from Guanabara, Minas Gerais, Rio de Janeiro and São Paulo differ from other specimens in having more dorsally directed eyes and triangular shaped bodies. Within this area, the northernmost specimens from Belo Horizonte, Minas Gerais are distinctive in that none of the individuals have distinct, small dark spots, many individuals are finely mottled, and some specimens have C category disks. The southernmost demes from the state of Parana are distinctive from the remaining populations in that many of the individuals have broad, light dorsolateral stripes.

Distribution (Fig. 24)—Range: Southeastern Brasil from Minas Gerais to Parana, sea level to 1500 m.

Etymology—The species is named for Werner C. A. Bokermann in recognition of his contributions to the study of frogs of the genus *Leptodactylus*.

Leptodactylus hylaedactylus (Cope)
Figure 25, 26

Cystignathus hylaedactylus Cope, 1868:115 (Type locality, Probably Peru, Napo or upper Marañon. Holotype ANSP 2240, male).

Leptodactylus diptyx Boettger, 1885:32-33 (Type locality, Paraguay. Lectotype BMNH 1947:2.17.47, male).

Leptodactylus glandulosus Cope, 1887:52-53 (Type locality, Brasil: Mato Grosso, Chupada, 30 mi NE Cuyata, nr. headwaters of Xingu. Lectotype ANSP 10275, juvenile).

Leptodactylus hololius Boulenger, 1918:430-431 (Type locality, Peru: Río Marañon, Pebas. Holotype BMNH 1915.3.9.13, female).

Leptodactylus minutus Nobel, 1923:295-297 (Type locality, British Guiana, Bartica District. Holotype AMNH A-13495, female).

Leptodactylus poeppigi Melin, 1941:59-60, Fig. 33 (Type locality, Peru: San Martín; Roque. Holotype Ba. Ex. 507, female).

Leptodactylus melini Lutz and Kloss, 1952:639-640 [Substitute name for *Leptodactylus rugosus* Melin, 1941:58-59, Fig. 32] (Type locality, Brasil: Amazonas; vicinity of Manaos. Holotype Ba. Ex. 506).

Diagnosis—The other species of the Marmoratus group in addition to *L. hylaedactylus* with toe tips not developed into flattened disks are *L. bokermanni* and *L. martinezi*. *L. hylaedactylus* does not have four longitudinal rows of symmetric dark spots as does *L. martinezi*. Many individuals of *L. hylaedactylus* have a mid-dorsal stripe extending from above the anus to the middle of the body or the snout, no *L. bokermanni* do; *L. hylaedactylus* larvae lack a spiracle and denticles, *L. bokermanni* larvae have a spiracle and denticle rows.

Summary of characteristics—Adults: Dorsal outline of snout subovoid or subelliptical in females, subelliptical or pointed in males; snout rounded in profile in females, rounded or rounded-acute in males; female snout ratio .672 ± .052, male snout ratio .723 ± .065; canthus rostralis indistinct; loreal very slightly concave or obtuse in cross section; tympanum distinct, greatest diameter equal to, just less than, or just greater than ½ diameter of eye; male vocal slits elongate, very slightly oblique to jaw or parallel to jaw; vocal sac single, internal, or a fold along margin of jaw to forearm; vomerine teeth in obtuse to transverse (usually) series, posterior to choanae; head length 38.0 ± 1.6% S–VL; head width less than length, 34.3 ± 1.4% S–VL; interorbital distance 8.8 ± .8% S–VL; length of the first finger equal to, just greater than, or just less than length of second finger; dorsum smooth or with ridges and warts, rarely with dorsolateral folds, most males with white-tipped tubercles profused over posterior dorsum, females without such tubercles; females without distinctive glands, males lacking distinctive glands or with paired, small oval glands at angle of jaw, just in back of axilla, in groin, and on either side of anus on hindlimb; toes usually with tips expanded, but not distinctly disklike (Fig. 1B), some toes lacking expanded tips (Fig. 1A) or with distinct disks (Fig. 1C), if with distinct disks, rounded, not flattened (Fig. 5B); toes free; subarticular tubercles moderately developed or pronounced; line of tubercles forming a metatarsal fold or absent; weak, sinuous or almost straight tarsal fold extending ¾ to ⅞ length of tarsus, smooth or with white-tipped tubercles; lower tarsus and sole of foot scattered or profused with white-tipped tubercles; female size 23.2 ± 2.1 mm S–VL, 31.0 mm maximum, male size 22.7 ± 1.5, 26.2 mm maximum; femur 41.0 ± 2.7% S–VL; tibia equal to or (usually) greater than femur, 44.6 ± 2.3% S–VL; foot longer than tibia or femur, 50.0 ± 3.4% S–VL; dorsal pattern commonly uniform (Fig. 2E), with indistinct marks (Fig. 2C), or distinctly spotted (Fig. 2B) rarely blotched (Fig. 2D), most individuals lacking light dorsolateral stripes, some with a narrow, light dorsolateral stripe, rarely with broad, light dorsolateral stripes, light mid-dorsal pin stripe from snout to above anus to absent, rarely with a broad light stripe from tip of snout to above anus to sacral region; throat and belly immaculate or scattered with melanophores, ventral edges of throat, belly, femur, tibia (or entire surface) scattered with melanophores, usually not distinctly mottled, some males with black vocal folds; posterior face of thigh mottled to uniform.

Larvae: Nostril midway between eye and tip of snout or nearer snout; distance between nares equal to interorbital distance; eye large, diameter 15.2 ± 1.6% body length; mouthparts subterminal; oral papillae in single row; oral disk entire; oral disk width 18.0 ± 1.6% body length; anterior oral papilla gap 82.5 ± 5.8% oral disk width; no denticles on tooth rows; beak weakly developed; no spiracle; dorsal fin origin at body-tail juncture, or origin on tail, posterior to body-tail juncture; tail height less

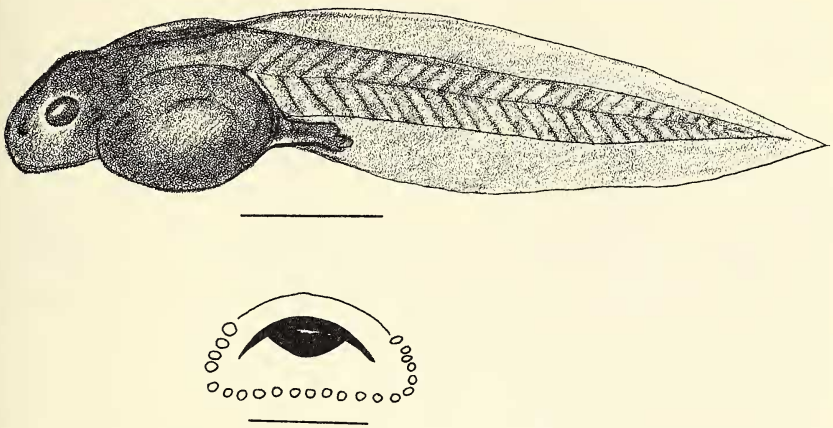

FIGURE 25. Lateral view and mouthparts of larva of *Leptodactylus hylaedactylus*. Upper line equals 1 cm, lower line equals 1 mm.

than, equal to, or greater than body height; tail tip elongate and rounded to pointed; anal tube median; dorsum with uniform pattern, gray to brown in preservative; venter with suffusion of melanophores on throat region, few melanophores on belly, no melanophores on anal tube; no melanophores on tail fins, scattered melanophores on upper two thirds of tail musculature; total length largest specimen, stage 34, 13.2 mm, stage 40, 12.6 mm; body length 36.7 ± 3.1% total length.

Geographic variation—The northernmost populations (Venezuela, Guyana, Surinam, French Guiana, and Amapá (part), Brasil) are distinctive from the remaining populations in having a high frequency of dorsal spotting (B category), a high frequency of narrow dorsolateral stripes that do not reach the eye (B category), and no instances of broad mid-dorsal stripes (E or G category). Andean slope populations from Peru and Bolivia are relatively homogeneous and are not distinctive from other populations. Populations from the Brasilian state and territory of Acre and Rondônia and from the state of Mato Grosso are distinctive both from other samples and among themselves (see analysis of form II specimens).

Distribution (Fig. 24)—Range: The species occurs from northeastern South America, central and southern Amazonia and south central Brasil. The known elevational range is sea level to 500 m. Dr. Avelino Barrio has recently collected material of the Marmoratus group from northern Argentina and kindly allowed me to examine the specimens. Morphologically, they are *L. hylaedactylus*. Dr. Barrio is preparing a paper on the specimens describing their morphology, mating call, ecology, and karyotype.

Localities—BOLIVIA. *Beni:* Upper Beni, below Huachi, UMMZ 74817; Cachuela Esperanza, 150 m, UMMZ 67738; Huachi, 250 m, MCZ 12900-1, 15578-81, UMMZ 64110-1, 64114; Ivon, UMMZ 74818; Lake Rogoagua, 200 m, UMMZ 64115; Puerto Almacen, 260 m, AMNH 72380; 4-5 km from confluence of Río Blanco and Río Itenez, AMNH 79093; Río Marmoré, nr. Guajara-Mirim, 160 m,

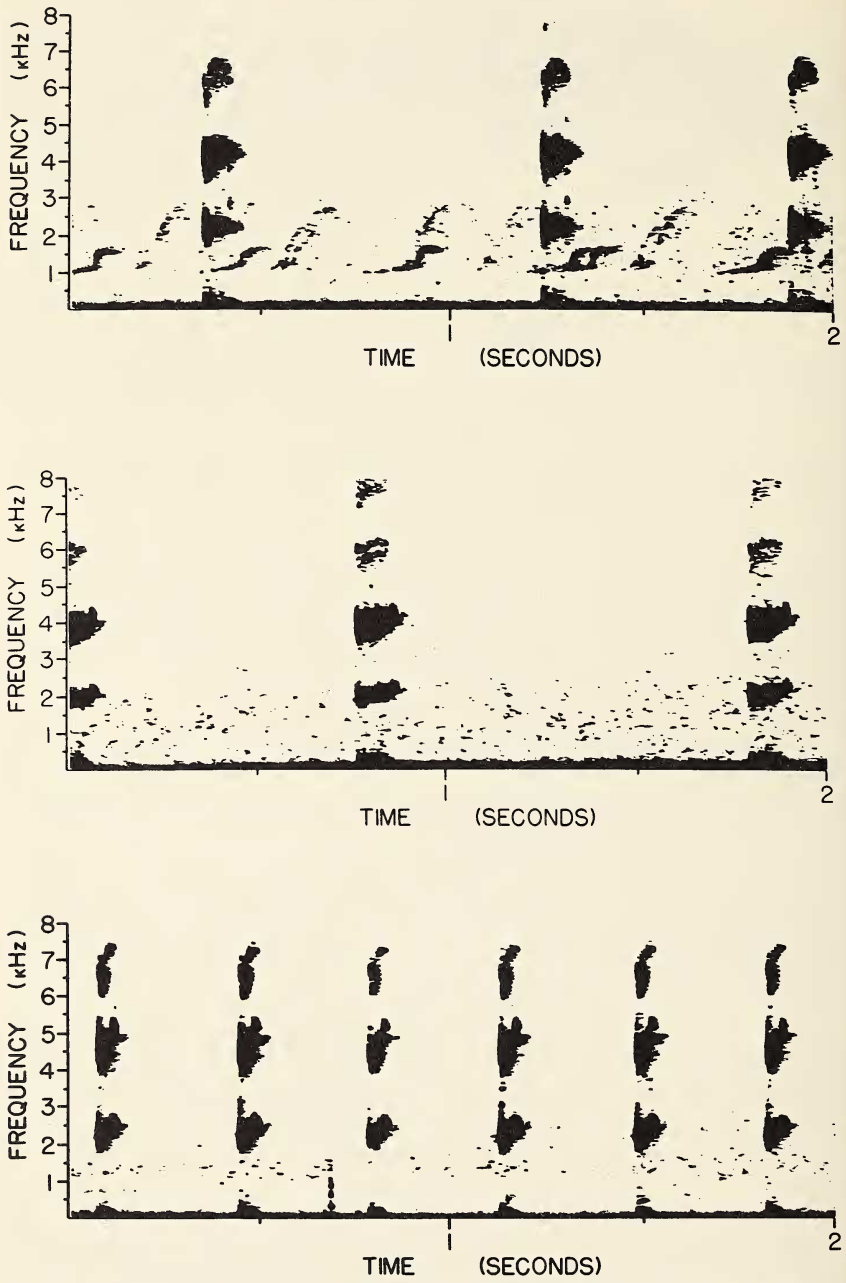

FIGURE 26. Audiospectrograms of *L. hylaedactylus*. Upper call from specimen WCAB 15091, Brasil, Mato Grosso, Sto. Antonio Leverger, temperature 29°C; middle call from specimen WCAB 15139, Brasil, Goiás, Jatai, temperature 26°C; lower call probably from specimen WCAB 15550, Brasil, Mato Grosso, Chapada dos Guimaraes, temperature 19°C.

CM 2665; Trinidad, AMNH 79091-2. *Cochabamba:* Sta. Elena, UMMZ 64112. *La Paz:* Lower Bopi, UMMZ 64113. *Santa Cruz:* Buenavista, 500 m, AMNH 34012, 34016, 34072, MCZ 12898-9, 15582, 15584, UMMZ 64031A, D–I, K–P, 64032A, 64033A–C, 64034, 64035A, B, 64036A–E, 66476, 66493E, G, 66494A, B, D, 66501.

BRASIL. Acre: Feijó, 249 m, WCAB 1263; Placido de Castro, DZ 6521, 6522, 6524; Tarauacá, WCAB 1387, 1389-90, 2513, 2855. *Amapá:* Mazagão, WCAB 19136-7, 35966; Oiapoque River, MCZ 25722, USNM 11511-2, 115514, WCAB 5614; Rio Tracajatuba, WCAB 19006; Serra do Navio, 220-300 m, WCAB 35243-4. *Amazonas:* Benjamin Constant, DZ 24890-92, 24893-6; Ducke Reserve, near Manaus, KU 129930-3; Itapiranga, DZ 27756; Manaus, AMNH 51756-9 (specimens referred to this species, although poor condition precludes positive identification); Ponta Negra, Negro River, DZ 24879-84; Puraquequara River (mouth) affl. Amazonas, DZ 24875-6. *Goiás:* Jatai, WCAB 15139. *Mato Grosso:* Chapada dos Guimaraes, 800 m, WCAB 15550; Pôrto Murtinho, UMMZ 76081 (specimen referred to this species, although poor condition precludes positive identification); Sto. Antonio Leverger, 100 m, WCAB 15091-2; Urucum, S. of Corumba, FMNH 9180-1, 9203-4, 9237. *Pará:* Belém, 20 m, WCAB 2014; Cachimbo, 500–600 m, DZ 21938; IPEAN, 3 km E Belém, KU 127339, 127353, 127356, 127358, 127365, 127370, 127376, 127378-9, 127391; Obidos, KU 129929. *Pernambuco:* Recife, DZ 25027. *Rondônia:* GuajaraAssu Falls, FMNH 64238; Igarapé Marmelo, WCAB 9846-51, 9854-5, 9859; Nhambiquara, WCAB 13279; Pôrto Velho and vicinity, 60 m, DZ 16350-1, UMMZ 64119D, F, WCAB 10709, 31721-3, 34103.

COLOMBIA. *Amazonas:* Leticia, 275 m, KU 124743.

FRENCH GUIANA. Cacao, LG 124; Cayenne, sea level, LACM 44280, LG 34; Crique Gabrielle, LG 126; Regina, 25 m, LACM 42082-3 (larvae), 44282-378; Roura, LG 877.

GUYANA. *Demerara:* Dunoon, 20 m, UMMZ 52506. *Essequibo:* Kartabo, 10 m, AMNH 39671, 39696; Marudi, 250 m, AMNH 46565-8 + 4; Membaru Creek, upper Mazaruni River, UMMZ 85148-9; Yarikita River, mouth and Haul Over, UMMZ 83581-2.

PERU. *Amazonas:* Mamayacu, Río Cenipa (trib. of Marañon), AMNH 42414. *Huanuco:* Divisoria, FMNH 56318; Hac. Pampyacu, MCZ 22810-9, 82199-204, UMMZ 83093(4); Tingo María, WCAB 36498. *Junín:* Río Perene, MCZ 22878-81. *Loreto:* Cumaría, AMNH 42799; Igarapé Champuia, Curanua Riv., DZ 10343-8; Iparia, MCZ 75032, 75034; Marañon, mouth of Río Pastaza, 150 m. AMNH 42228; Parinari (Marañon), AMNH 43437; Pucallpa, Río Ucayali, FMNH 56321; Río Pisque, AMNH 43548, 43561; San Regis, on Río Marañon, AMNH 42059, 42487; Suhuaya, nr. Contamana on Río Ucayali, AMNH 42075. *Pasco:* Iscozazin Valley, Pan de Azucar, 380 m, LACM 40651-53, 40655-6, 40658-9; Oxapampa, Nevati Mission, USNM 166769-70.

SURINAM. *Marowijne:* Langaman Kondre, DZ 24757. *Nickerie:* Sipaliwini, RM 16719, 16721, 16723, 16755. *Suriname:* Brownsweg, RM 16734; Lelydorp, RM 16731; Paramaribo, AMNH 77464, MCZ 17925, RM 16732-3, 16735, 16738.

VENEZUELA. *Monagas:* Caripito, ± 50 m, AMNH 70654-64, USNM 117090-1.

FIGURE 27. Distribution of *Leptodactylus andreae* (circles), *L. marmoratus* (triangles), and *L. martinezi* (squares). Solid circles indicate two homogeneous population units of *L. andreae,* one along the Andes, the other of North Central South America. Open triangle indicates distinctive island population of *L. marmoratus*.

Leptodactylus marmoratus (Fitzinger *in* Steindachner)
Figure 28

Adenomera marmorata Fitzinger *in* Steindachner, 1867:37, Taf. III, Figs. 5–8 (Type locality, Brasil. Holotype Vienna 16453, male).

Leptodactylus nanus Müller, 1922: 168-179, Figs. 4–6 (Type locality, Rio Novo, Santa Catarina, Brasil. Lectotype Munich 661/1920, a female).

Leptodactylus trivittatus Lutz, 1926:151, Plate 32, Figs. 14, 15 (Type locality, Campo Belo, Alto da Serra De Cubatao, Brasil. Lectotype USNM 96943, a juvenile).

Diagnosis—The only other species in the Marmoratus species group in addition

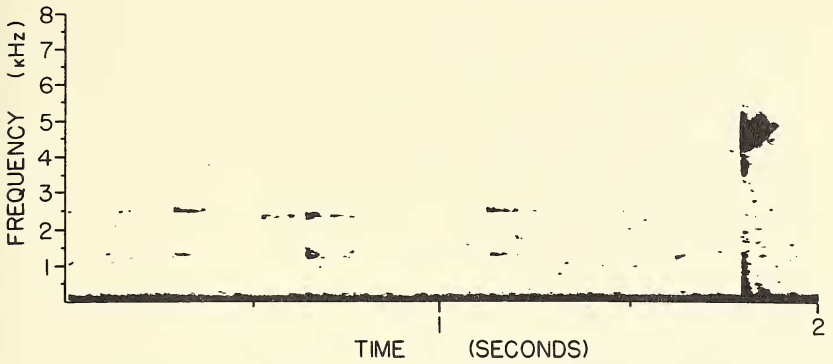

FIGURE 28. Audiospectrogram of *L. marmoratus*, Brasil, Guanabara, Tijuca, temperature 22°C. No specimen.

to *L. marmoratus* with flattened toe disks is *L. andreae*. No individuals of *L. marmoratus* have dorsal longitudinal stripes, some *L. andreae* have such stripes; some *L. marmoratus* have light mid-dorsal pin stripes extending from above the anus to the snout or shoulder region, almost no *L. andreae* have the pin stripe, if present, extending beyond the sacral region.

Summary of characteristics—Adults: Dorsal outline of snout nearly semicircular, rounded, subovoid, or subelliptical in females, subovoid, subelliptical, or pointed in males; snout rounded in profile in females, rounded or rounded-acute in males; female snout ratio .687 ± .046, male snout ratio .712 ± .052; canthus rostralis indistinct; loreal slightly concave or obtuse in cross section; tympanum distinct, equal to or just less than ½ diameter of eye; male vocal slits elongate, slightly oblique to jaw or parallel to jaw, vocal sac single, internal, or a fold along margin of jaw to forearm; vomerine teeth in transverse (usually) or slightly obtuse series posterior to choanae; head length 38.4 ± 2.2% S–VL; head width less than length, 33.6 ± 1.1% S–VL; interorbital distance 9.0 ± 0.8% S–VL; length of first finger equal to, just greater than, or just less than length of second finger; dorsum smooth or with white-tipped tubercles on posterior portion in individuals of both sexes, ridges or warts, or rarely with distinct dorsolateral folds; small, round or oval paired glands present at angle of jaw and on either side of anus on hind limb present or absent; toes usually with distinct, flattened disks (Figs. 1C, D; 5A); toes free; subarticular tubercles moderately developed; weak line of small white-tipped tubercles forming a metatarsal fold or absent; weak, almost straight tarsal fold extending ⅜ — ⅞ length of tarsus with series of very small tubercles; lower surface of tarsus and sole of foot profused with white-tipped tubercles; female size 21.9 ± 1.7 mm S–VL, 27.9 mm maximum, male size 20.8 ± 1.8 mm S–VL, 26.0 mm maximum; femur 40.4 ± 3.0% S–VL; tibia equal to or (usually) longer than femur, 44.2 ± 2.2% S–VL; foot longer than either femur or tibia, 49.5 ± 2.7% S–VL; dorsal pattern commonly uniform (Fig. 2E) or with indistinct marks (Fig. 2C), rarely distinctly spotted (Fig. 2B) or blotched (Fig. 2D), very rarely lined (Fig. 2A), most individuals lacking light dorsolateral stripes, a few with narrow stripes, several with well defined light stripes from eye to groin (Fig. 12C), light

mid-dorsal stripe ranging from present from tip of snout to anus to absent; throat scattered with melanophores or center of throat and belly immaculate, ventral edges of throat, belly, femur, and tibia mottled; posterior face of thigh mottled to uniform.

Geographic variation—Mainland populations appear to form a north-south cline with respect to size and mid-dorsal stripes. The larger individuals are in the north (maximum male S–VL about 24 mm, female S–VL about 25 mm) the smallest individuals are in the south (maximum male S–VL about 19.5 mm, female S–VL about 20 mm). No individuals from the north (Guanabara, Rio de Janeiro) have light mid-dorsal pin stripes extending beyond the sacral region anteriorly. In São Paulo, some individuals have light mid-dorsal pin stripes extending to midbody (B category). In Santa Catarina some individuals have B category mid-dorsal stripes as well as some individuals having a continuous pin stripe from the snout to the vent (C category). The deme on Alcatrazes Island is distinctively larger than any other island or mainland population (male S–VL to 26 mm, female S–VL to 27.9 mm).

Distribution (Fig. 27)—Range: Southeast Brasil from the states of Guanabara and Rio de Janeiro to the state of Santa Catarina. Known elevational range, sea level to 850 m.

Localities—BRASIL. *Guanabara:* Rio de Janeiro, Cosme, USNM 119000-3; Jacarepagua, USNM 97472-85; Sumré, 850 m, WCAB 12984; Tijuca, 400 m, AMNH 36257, MCZ 15846, UMMZ 68792, 104275, 104278, USNM 81132, 96300-2 + 10, WCAB 14342, 16641, 16643-4, 16646, 16932, 17357, 18943, 30564. *Parana:* Volta Grande, USNM 125505, 125531-2. *Rio de Janeiro:* Angra dos Reis, USNM 70591-2, 96519; Barro Branco, UMMZ 104263, USNM 133009; Grande Island, DZ 25101; Guanabara, DZ 7, 8, 13, 22, 27, 35, 38, 148; Itatiaia National Park, DZ 4130, Vienna 4490; Petropolis, USNM 96417, 96430, Vienna 15802, 19413:1, 2; Pico de Tijuca, USNM 133010; Represa Rio Grande, Guanabara, 50 m, WCAB 7589-643, 9380, 22727, 14120-21; Rio de Janeiro, USNM 97235; Teresópolis, USNM 97682. *Santa Catarina:* Rio Humboldt, AMNH 15569-70, FMNH 6473, MCZ 8841-2, 11680, 19510-9, 12903, 82205-10, USNM 66583, 118177-8; Rio Vermelho, WCAB 3416-7, 5105; São Bento do Sul, WCAB 6104. *São Paulo:* Alcatrazes Island, DZ 24163, 24172, 24175, 24177, 24182, 24205-6, 24231-2; Alta da Serra de Cubatão, USNM 97858; Boracea, USNM 129175; Buzios Island, DZ 24140; Caraguatatuba, DZ 24291; Cubatão, 800 m, DZ 495, 1972, WCAB 2425-6; Est. Biol. Boracéia, Salesopolis, DZ 2733, 2745-6, 3373, 3375, 24293; Itanhaem, DZ 626, 10931; Itapetininga, DZ 25430-1; Paranapiacaba, 800 m, DZ 10783-4, WCAB 6581, 6849, 11957; Piassaguera, DZ 771, 914, 2041, 2042, 2043; Rio Grande, DZ 658; São Paulo, 800 m, DZ 4218, 6386, 6469, 9372, 10578-80, 15662, WCAB 45104-6; São Sebastião Island, 50 m, CM 33439, DZ 6408-19, 24276-83, FMNH 67257-60, KU 74217-21, WCAB 4907-8, 8210-20, 8222-6, 8821-30, 8898-900, 9389, 13643-53; São Vicente, 5 m, DZ 4155, WCAB 7316.

Leptodactylus martinezi Bokermann

Leptodactylus martinezi Bokermann, 1956: 37-40, Figs. 1-4 (Type locality Cachimbo, Pará, Brasil. Holotype WCAB 71, male).

Diagnosis—Leptodactylus martinezi is the only species in the Marmoratus

species group that has four symmetrically arranged rows of longitudinal spots. The dark spots of other species, if present, are never thus arranged.

Summary of characteristics—Adults: Dorsal outline of snout subovoid or subelliptical in females, subelliptical or pointed in males; snout profile rounded; female snout ratio .736 ± .071, male snout ratio .95; canthus rostralis indistinct; loreal very slightly concave or obtuse in cross section; tympanum distinct, greatest diameter equal to or just less than ½ diameter of eye; male vocal slits elongate, very slightly oblique to jaw; vocal sac single, internal; vomerine teeth in transverse series, posterior to choanae; head length 39.4 ± 1.6% S–VL; head width less than length, 32.8 ± 2.1% S–VL; interorbital distance 8.1 ± .9% S–VL; length of first finger equal to or just greater than length of second finger; dorsum smooth or warty, white-tipped tubercles posteriorly in a few individuals of both sexes; much of dorsal and lateral surfaces glandular appearing, but no distinct glands; toe tips pointed or slightly swollen (Fig. 1A, B); toes free; subarticular tubercles moderately developed or pronounced; line of white-tipped tubercles forming a metatarsal fold or absent; tarsal fold weak, sinuous or almost straight, extending ⅝ to ⅞ length of tarsus, tuberculate; female size 22.3 ± 1.1 mm S–VL, 24.5 mm maximum, male size 23.1 mm, 23.4 mm maximum; femur 39.3 ± 3.6% S–VL; tibia longer than femur, 46.0 ± 1.2% *S*–VL; foot longer than tibia, 50.8 ± 1.8% S–VL; dorsal pattern of symmetrically arranged distinct dark spots in four longitudinal rows, light, thin mid-dorsal stripe from tip of snout to above anus, no light dorsolateral stripes; ventral surfaces scattered or profused with melanophores, not mottled; posterior face of thigh mottled.

Distribution (Fig. 27)—Range: *L. martinezi* is found in Central Brasil. The known elevational range is 200–600 m.

Localities—BRASIL. *Goiás*: Sta. Isabel, Bananal Island, DZ 25325. *Mato Grosso:* Mato Verde, DZ 25320-1, 25242-9, 25322-4; São Domingos, Rio das Mortes, 200 m, DZ 25216. *Pará:* Cachimbo, 500–600 m WCAB 71-2.

An Artificial Key to the Adults of Members of the Marmoratus Group

The key is provided only as an aid to identification. Because of the subtle differences separating the species, extensive use of the analysis section must be used for verification.

1A. Dorsal pattern of four longitudinal rows of symmetrically arranged dark spots ..... *L. martinezi*

1B. Spots, if present on dorsum, never symmetrically arranged in four rows ... 2

2A. Toe tips pointed or expanded; if disked, disks are round, not flattened .3

2B. Toe tips expanded into flattened disks 4

3A. No individuals with a light mid-dorsal stripe extending from above the anus to the middle of the body; southeast Brasil ..... *L. bokermanni*

3B. Many individuals with light mid-dorsal stripes extending from above the anus to the middle of the body or the snout; northeastern South America, central and southern Amazonia, south central Brasil ..... *L. hylaedactylus*

4A. Some individuals with a striped dorsal pattern; almost no individuals with light mid-dorsal pin stripe extending from above the anus to beyond the sacral region; north, central, and western South America east of the Andes ..... *L. andreae*

4B. No individuals with striped dorsal patterns, some individuals with light mid-dorsal pin stripe extending from above the anus to beyond the sacral region; southeast Brasil ..... *L. marmoratus*

RELATIONSHIPS

One member of the Marmoratus group is clearly distinctive from the others: *L. martinezi*. The remaining four species form a closely related complex. The working hypothesis of the previous analysis was that the allopatric populations form species pairs: *L. hylaedactylus* and *bokermanni; andreae* and *marmoratus*. The distribution of toe tip character states supports this arrangement (Fig. 29D). The distributions of other character states agree in part only or not at all, however: 1) Dorsal pattern. *L. bokermanni* and *hylaedactylus* are similar in sharing states B, C, and E, *L. andreae* and *marmoratus* are similar in sharing states C, D, and E. State A is found in some *L. andreae,* only one *L. marmoratus* examined approaches state A (Fig. 29A). State B is extremely rare in *L. andreae,* more common in *marmoratus* (Fig. 29D). More interesting is that no *L. bokermanni* have state D patterns, while state D is rarely present in *hylaedactylus* (Fig. 29E). 2) Dorsolateral states. All four species have states A and B. *Leptodactylus hylaedactylus* does not have the typical state C category. The few light dorsolateral stripes that are present in *L. hylaedactylus* extend from the shoulder region to the groin. *Leptodactylus bokermanni, andreae,* and *marmoratus* have the C state (Fig. 29C). 3) Mid-dorsal stripes. *Leptodactylus bokermanni* and *andreae* share state A, D, and F, *L. hylaedactylus* and *marmoratus* share states A, B, C, D, and F (Fig. 29B). The composite of all the characters is a mosaic which does not provide any clear indications of relationships among the four species.

In the section, recognition of "non-dimensional" species, a single instance of apparent hybridization was noted between *L. hylaedactylus* and *L. andreae*. Hybridization data are difficult to interpret. In fact, one could interpret the data as either implying that *L. hylaedactylus* and *L. andreae* were the most closely related species pair or the most distantly related species pair. If the former were true, then the four species would represent an interesting case of parallel speciation involving similar adaptive types. Further speculation should await the availability of more data, particularly from life histories and karyotypes.

DISTRIBUTION

The forests of southeast Brasil contain two species, *L. bokermanni* and *marmoratus*. Two species are found in Amazonian and Orinocoan Forests, *L. andreae* and *hylaedactylus*. It appears that *L. andreae* is confined to these forest regions. The only exception is a single possibly erroneous record from forest west of the Andes. *Leptodactylus hylaedactylus* also occurs in the drier forests of southern Bolivia and Mato

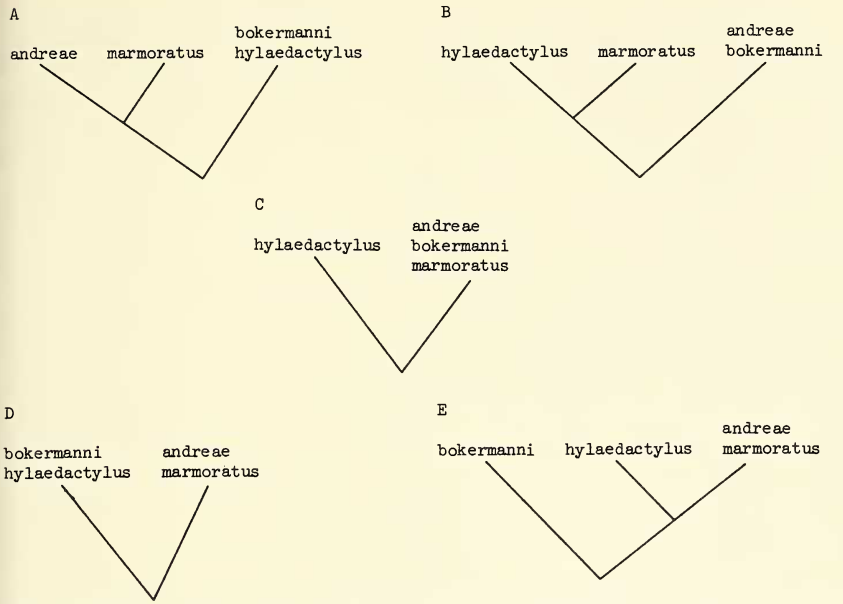

FIGURE 29. Phenetic character trees for four species of the Marmoratus group. Also see text.

Grosso, but the species is definitely excluded from the Chaco. A single specimen from Recife, Pernambuco, Brasil is frustrating. As far as habitat is concerned, the species should occur there. But why there should be only a single record available from the east Brasilian forest strip seems odd. The region has been visited by collectors and other species of *Leptodactylus* are known from there (Heyer, 1970a). The only species with a distribution confined to dry forests is *L. martinezi* in central Brasil. *Leptodactylus andreae* and *L. marmoratus* are found in two types of habitat: primary forest and house gardens (Marty Crump and William E. Duellman, personal communication, Lutz, 1947:248). These two types of habitats suggest that the frogs are limited by soil moisture. The soil must be sufficiently moist so that larvae do not desiccate within the chambers. The soil must not be flooded, however, as flooded soil would not permit the construction and maintenance of the chambers. It seems probable that the members of the Marmoratus group evolved in primary forests and have secondarily invaded gardens.

Refugia—Comparison of the patterns of differentiation in the Marmoratus group with results of Vanzolini and Williams' (1970) analysis of the *Anolis chrysolepis* species group indicates some striking parallels. Vanzolini and Williams demonstrated the existence of four core areas within the geographic distribution of *A. chrysolepis*. These core areas contain populations that are rather uniform, but the regions between core areas have heterogeneous populations. They reason that the core represented forest refugia during dry Pleistocene periods, the populations within each refugium became homogeneous and with more mesic climates, such as now, the species have spread out from the refugia.

Before comparing results of core area distributions, it is instructive to compare and contrast the distributions and evolutionary origins of the *Anolis chrysolepis* and Marmoratus species groups. *Anolis chrysolepis* occurs throughout northern Venezuela. Members of the Marmoratus group are absent over much of northern Venezuela. The Marmoratus group does not provide a test for Vanzolini and Williams' core area III which covers this region. At the other extreme, *Anolis chrysolepis* does not occur in southeast Brasil, so no information from that study is available for comparison. What remains for comparison is Vanzolini and Williams' core areas I, III, and IV. Members of the *Anolis chrysolepis* group are relatively recent invaders of South America, with their evolutionary origins in Middle America and Mexico. Members of the Marmoratus species group are strictly South American, probably having undergone their total evolutionary history *in situ*.

The distribution patterns of figures 24 and 27 are readily comparable with Vanzolini and Williams' core areas. *Leptodactylus andreae* (Fig. 27) demonstrates the presence of two core areas, corresponding with core areas I (Surinam, French Guiana, and Amapa, Brasil) and III (east Andean slopes of Colombia, Ecuador, and Peru) of Vanzolini and Williams. *Leptodactylus hylaedactylus* (Fig. 24) demonstrates clearly a core area corresponding with core area I of Vanzolini and Williams. The other region delimited in figure 24 is a heterogeneous area, which by default leaves the east Andean slope populations a homogeneous group, although it is not particularly distinctive in any regard. As a homogeneous assemblage, the east Andean slope populations of *L. hylaedactylus* correspond to core area III of Vanzolini and Williams. Vanzolini and Williams suggested that their core area III was actually a composite of three smaller core areas which have merged. The combined distributions of *L. andreae* and *L. hylaedactylus* substantiate that hypothesis. The absence of *L. hylaedactylus* from Ecuador and the east Andean slopes of Colombia is easiest explained if *L. hylaedactylus* was never present in the northern refugia within core area III. The distribution of *L. martinezi* coincides with core area IV of Vanzolini and Williams. The core areas deduced from detailed geographic analyses of the *Anolis chrysolepis* and Marmoratus groups coincide almost too perfectly. The validity of the core areas is attested to by the fact that organisms with different evolutionary origins have similar core area patterns. The critical similarity between the two groups of organisms is that they are both forest groups.

Vuilleumier (1971), in reviewing the Pleistocene changes in fauna and flora of South America noted the relative goodness of fit between Haffer's (1969) proposed forest refugia based on bird studies and Vanzolini and Williams' (1970) proposed refugia. The results of this study are consistent with Vanzolini and Williams' results and differ from Haffer's in the same way as Vanzolini and Williams' differed. Vuilleumier (1971) also indicated that Muller (1968) had proposed a forest refugium in Southeast Brasil, the Serra do Mar refugium.

Leptodactylus wagneri: A contrast—In a previous study (Heyer, 1970a), analysis of the geographic distribution of certain character states within *L. wagneri,* which is distributed throughout the same region as the *Anolis chrysolepis* group and along east coastal Brasil, did not have any patterns indicative of core areas or refugia. Rather, the only characters with significant geographic variation were clinal in nature. Members of

the Marmoratus group differ from *L. wagneri* in one significant ecological way. While the Marmoratus group members are forest forms, *L. wagneri* is more of a clearing or ecotonal species (Heyer and Bellin, 1973). *Leptodactylus wagneri* is associated with forests in its distribution pattern, but within the general forested regions it is found in clearings, or to be more precise, in the most arid microhabitats within the forests (Heyer and Bellin, 1973). Thus *L. wagneri* by the nature of its ecology should not be restricted to forest refugia during xeric periods, but in fact, its population should be maximum at such times providing the climate is not too extreme.

Ecological and Evolutionary Implications

Ecological data are scarce for all species. Heyer and Silverstone (1969) indicated that in French Guiana, *L. hylaedactylus* and *andreae* (reported as *marmoratus*) were ecologically distinct. Collections from the localities where *L. bokermanni* and *marmoratus* or *L. hylaedactylus* and *L. andreae* have been taken together are suggestive that ecological differences are found thoughout the ranges of the species pairs. With a single exception, one species is common, the other rare at sympatric sites. This may well be due to the bias of individual collectors, collecting one habitat type more thoroughly than another.

Lutz (1947) has discussed the terrestrial life history of *L. marmoratus* (as *L. nanus* and *trivittatus*). The eggs are placed in terrestrial chambers, hatch, and metamorphose without leaving the chamber. The yolk stores are sufficient to carry the larvae through metamorphosis without the necessity of feeding. Unfortunately, Lutz did not comment on the morphology of the larvae. Heyer and Silverstone in describing the larvae of *L. hylaedactylus* (1969) suggested that *hylaedactylus* probably do not feed as larvae as in *marmoratus* because the larvae had large yolk stores, degenerate mouthparts, and no spiracle. The larvae of *L. bokermanni* appear to have functional mouthparts (although the denticles are at best weakly developed) and a spiracle is present. There are fewer yolk stores in the stage 30 larvae of *L. bokermanni* than in the stage 40 larvae of *L. hylaedactylus*. In the *L. bokermanni* larvae the yolk is visible inside the few large coils of the intestine. The fact that the intestine is composed of few large coils filled with yolk at stage 30 is indicative that the individuals are still being nourished by the yolk. Later staged larvae may have to utilize additional food resources, however. A female *L. bokermanni,* WCAB 34465, had about 18 large eggs in the body. An attempt was made to determine the variation in clutch size from the museum materials, but it proved impractical. It is obvious that a female starts with 40 or 50 ova of small size. Some ova are reabsorbed while others grow and it is not possible to determine where the process stops in the preserved specimens. Exact data on clutch size will have to be gathered from nests in the field. The greatest number of large eggs examined was 18 in the *L. bokermanni* female mentioned above. The smallest number of large eggs examined was about 5 in a single female. There appears to be a considerable range in clutch size in the group. The species with the largest clutches may have larvae that are not as terrestrially adapted as the species with smaller clutch sizes (and concomitant larger individual egg size). At any rate, the presence of the less specialized *L. bokermanni* larvae as compared to *L. hylaedactylus* larvae

supports the earlier hypothesis (Heyer, 1969) that evolution towards terrestriality has occurred independently in the Marmoratus group on one hand and the other species groups of *Leptodactylus* on the other.

I have previously suggested that the foam nest as found in members of the genus *Leptodactylus* has been in major response to arid conditions. This hypothesis is supported by the ecology of such forms as *L. wagneri* and *L. mystaceus* which breed in temporary ponds in environments where more stable ponds also occur (Heyer and Bellin, 1973). The breeding biology of the Marmoratus group has been a reponse to very different environmental conditions. In the tropical rainforest *(sensu lato)* the temporary pond or stream environments are less predictable than in tropical dry forests *(sensu lato)*. In dry forests, the rains may be sporadic, but usually occur at the same time of the year and the frogs are seemingly able to gauge the intensity of the rains, breeding at times of sufficient rainfall. In the rainforests the rains are more random and the frogs are not able to use them in a predictive manner. The terrestrial environment is more or less stable with respect to moisture throughout the year; if frogs were to become terrestrial, they could maintain breeding populations throughout the year. This is apparently what members of the Marmoratus group have accomplished through the mechanism of the foam nest. If these hypotheses are true, the foam nest of the Marmoratus group has evolved in response to mesic, unpredictable environments while the foam nest of the other *Leptodactylus* groups has evolved in response to xeric but predictable environments.

Leptodactylus andreae-hylaedactylus and *bokermanni-marmoratus* occur sympatrically over wide geographic areas. But there have doubtless been a series of many, separate encounters among the species pairs that occurred at the deme level. It is at the deme level, of course, where character displacement would operate to build premating isolating mechanisms between the species. Examination of the specimens from the several localities where two species occur together indicates that the displacement has not affected the same characters in the same ways. For example, at some localities there is a definite size difference between the species, but at other localities there does not appear to be a size difference. At some localities the toe disk development is distinctly different, at others it is not as nearly pronounced. In actuality, the morphological differences between the species pairs are so slight that they have been overlooked previously. One would expect the mating calls would be one of the first characters to diverge to maintain the species distinctness. But the divergence of mating calls has doubtless occurred many different times with many different demes with the recurrent pattern of expansion and contraction of ranges. Thus one might expect that the mating calls of the species pairs are distinct wherever the species occur sympatrically, but the characteristics of the mating calls within a species may demonstrate a complicated pattern when examined geographically.

RESUMEN

Se examinaron la distribución geográfica de ocho características de tamaño, forma, textura de la superficie de la piel, y coloración de las especies del grupo *marmoratus* del género anuro *Leptodactylus*. Una análisis de la distribución geográfica

de las características supracitadas indica que el grupo abarca cinco especies. En *Leptodactylus bokermanni,* una nueva especie de los bosques del sureste del Brasil, las puntas de los dedos no son dilatadas. En *Leptodactylus hylaedactylus,* que habita los bosques de Amazonia y el suroeste del Brasil, las puntas de los dedos no son dilatadas o son escasamente dilatadas. En *Leptodactylus andreae,* que se encuentra en los bosques de Amazonia y la región del Orinoco, las puntas de los dedos son dilatadas en la forma de discos. En *Leptodactylus marmoratus,* que se encuentra en los bosques del sureste del Brasil, las puntas de los dedos son dilatadas en la forma de discos. En *Leptodactylus martinezi,* que habita los bosques secos de la parte central del Brasil, las puntas de los dedos no son dilatadas. Hay una diagnosis y descripción de cada especie y una clave para la identificación. Se presenta la hipótesis de que el nido de espuma del grupo *marmoratus* y el de los otros grupos del género *Leptodactylus* se desarrollaron como resulta de distintas fuerzas de selección natural. En los otros grupos, el nido de espuma se desarrolló como resulta de un clima árido con fuertes lluvias esporádicas. En tal clima, se puedeasegurar el éxito de la reproducción mediante utilizar la lluvia como pronóstico de condiciones favorables. En cambio en el grupo *marmoratus* es posible que la lluvia no sea un buen pronóstico de éxito en la reproduccion. El ambiente de animales terrestres en bosques tropicales pluviales es relativamente estable en cuanto a la reproduccion. En el grupo *marmoratus,* el nido de espuma aparentemente se desarrolló como resulta de selección natural a favor de un modo de vida terrestre.

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